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Hearing in Vertebrates:

a Psychophysics Databook

Richard R. Fay

Hill-Fay Associates



**HEARING IN VERTEBRATES:
A Psychophysics Databook**

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With:
294 original figures
281 tables

**HILL-FAY ASSOCIATES
WINNETKA, ILLINOIS**



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This book is dedicated to the memory of
George A. Gourevitch,
my good friend and colleague in the study of animal psychophysics.

PREFACE

The idea for this book arose following an invitation to survey something of what was known about hearing (defined by behavior) in the mammal species most often used in auditory research as models for human hearing, at the mid-winter meeting of the Association for Research in Otolaryngology, Clearwater, Florida, 1987. The goal was not to review methodologies or to discuss reliability. The focus was rather on the data themselves; on the state of our knowledge about what animals hear and what they can discriminate. I had been asked to present similar reviews of animal hearing at other meetings since 1974. As interesting to prepare and as well received as they usually were, these reviews were a bit of a frustration. The problem is that once the figures (laboriously compiled and drawn) were projected on the screen and commented upon, they disappeared all too fast. The idea of publishing the reviews in a scientific journal often arose, but page limitations, forcing a restricted focus (e.g. frequency selectivity in selected mammals), restricted the number of enthusiastic readers. This, coupled with the fact that review papers have only marginal value in the academic marketplace, dampened my enthusiasm for journal publication.

It also seemed to me that the figures in many published reviews rapidly disappear as well. The reader is usually interested in a specific set of data which may or may not be found in any one review, and then in only graphical form. To make the comparison of immediate interest, the reader has to gather together several reviews and original papers, get out the calipers or digitizing pad, and spend a day or so drawing his or her own figures. This process is further impeded by the high cost of searching bibliographic databases, the pace of inter-library loan, and the often idiosyncratic and sometimes microscopic figures that many of us publish. In short, the usual review paper can help to orient the reader on a given topic, but much of the labor and quantitative struggle that went into compiling the numbers and creating the figures seems to get lost for those who want to make quantitative use of the reviewed data.

This book is an unusual review of the published literature on hearing in vertebrates. It is designed to give the reader rapid access to the bulk of the multidisciplinary literature, present experimental results as a set of numbers as well as graphically, and to be as comprehensive, as easy to use, and as useful as possible. With this, the reader can quickly determine which papers in the literature contain data of interest given the specific question at hand, and can immediately begin to extract and compare quantitative information. The scope of the book is such that it should help to define the state of the field; providing a sort of "snap-shot" of what is, and what is not known about animal hearing. It could be useful in helping the auditory scientist decide what experiments might be valuable to do, and what might not be, and in providing a "modeler" with the criteria for evaluating theories of perception based on structural or physiological data from a given vertebrate species.

An important feature of the book is that most all published psychophysical data of which I am aware are included (with the exceptions as described below). This lack of selectivity and discrimination on my part means that controversies regarding the best description of a given species' hearing capabilities, or the validity of certain conditioning and psychophysical methodologies can be dealt with in the largest possible comparative context by the reader, not by the reviewer. Sometimes, just by the weight of the combined data on a given topic (for example, the 13 audiograms for the chinchilla, and the five audiograms for the parakeet) questions on the validity of a particular experimental paradigm may be resolved. At the same time, the broad comparative context of this book helps to establish the general validity of animal psychophysics. For example, the long standing observation that humans have significantly lower frequency discrimination thresholds than other mammals such as the cat and monkey has suggested to some that the conditioning methods used with animals simply overestimate frequency discrimination thresholds. But now we have data showing that at least two mammals (the elephant and porpoise) and several birds discriminate frequency differences with an acuity equal to (or better than) the human. This argues against the notion of a general failure of methodology.

The data reviewed here also help provide a greater, biological context within which human hearing can be better understood. Human psychophysical data - far more extensive than for animals - are thus brought more solidly into biological science, and are made even more valuable and interesting. Animal psychophysics provides a necessary link between animal physiology and human perception and permits human psychophysics to have a greater and more quantitative role as a method in the neurosciences.

Acknowledgements

I could not have produced this book without the love, encouragement, and great patience of my wife Catherine and my children, Christian and Amanda. Countless hours on the PC at home earned me the affectionate title of "terminal man," and the two-fingered typing I did as "terminating."

Thanks are also due to the staff at the Parmlly Hearing Institute, including Chuck Wheelles, Scott Stubenvoll, Marilyn Larson, Beth Langer, Luann Kowar, and Cynthia Welther. I thank the inter-library loan service at the Loyola University Library for handling hundreds of requests efficiently and accurately.

I would not have attempted this book were it not for the availability of appropriate PC hardware (hard disks, graphics terminals, and a laser printer) and for appropriate text and graphics software including WordPerfect (WordPerfect Corporation), and Symphony and Freelance Plus (Lotus Development Corporation).

The writing of this book was also facilitated by the helpful comments and reprint contributions by my colleagues and friends George Gourevitch, Sheryl Coombs, Bill Shofner, Toby Dye, Bill Yost, Randy Brill, John Janssen, Art Popper, Bob Dooling, Joan Sinnott, Bill Clark, Henry and Rickye Heffner, Bill Stebbins, Dave Moody, Jim Miller, Ed Rubel, George Gerken, Wolf Plassman, Andreas Elepfant, Andrea Megela Simmons, Jim Simmons, Bill Ahroon, Peter Narins, Jim Saunders, Brian Pfingst, Lincoln Gray, Doug Webster, Glenis Long, and George Pollack.

Richard R. Fay
Chicago, 1988

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INTRODUCTION

The Uses of This Book

I hope that this review will be of value and interest to researchers and students in the many fields which combine to form hearing science. Those researchers in animal psychophysics will find a comprehensive, ready reference to the published work in their field. Auditory physiologists will find data to help in the design and interpretation of their experiments on the neural codes underlying the perceptions of the species they study. Those who study the biophysics and physiology of the ears of diverse animal species will have efficient access to the rather far-flung literature on the auditory perception of "their" species. Neuroscientists, engineers, and other modelers interested in the brain mechanisms underlying perception will have quantitative descriptions of system behavior that may help refine their questions and evaluate their models. Evolutionary biologists and anatomists will have a guide to the ultimate functional correlates of the structures they study. Animal behaviorists and experimental psychologists will have a reference for estimating the potential information content and likely discriminability of the stimuli they may use in controlling and analyzing behavior. Otolaryngologists and audiologists might discover among these data useful animal models for their study of auditory pathology and hearing impairment. Finally, those concerned with the management, breeding, and husbandry of different animal groups can use these data to help design and evaluate acoustical environments appropriate for given species.

Scope of the Book

This book presents psychophysical data on vertebrate hearing obtained from the published literature. The data presented here are in the form of new figures original to this book, and tables giving the numerical values of all plotted points. The book contains separate sections on the **Lateral Line System** (7 figures), **Fish Hearing** (62 figures), **Amphibians and Reptiles** (16 figures), **Birds** (63 figures), **Mammals** (over 115 figures), and **Comparisons among Vertebrates** (13 figures). In addition to data on hearing sensitivity, discrimination, and directional hearing, data are included on hearing development and infant hearing, aspects of echolocation, and the psychophysics of electrical stimulation of the auditory system. The book contains a **Topical Index** for each section and also combined for all vertebrates, a **Species Index** containing all scientific and common animal names with references to the kinds of data available for each, complete bibliographic references (placed on the text pages displaying the data derived from them, and as a combined **Bibliography**), a **Journal List**, and an **Author Index**. Introductions precede each section. A **Comparative Section** brings together selected data from different animal groups for comparison across all vertebrates.

Data on vertebrate hearing have been derived from original research papers, book chapters, theses, and, rarely, from abstracts or unpublished papers (e.g. papers presented at meetings). An attempt was made to obtain

the data from published research papers whenever possible, and references to theses, abstracts and unpublished papers are kept to a minimum.

An attempt was made to include all published auditory (and lateral line) psychophysical data for non-human vertebrates (183 species of fishes, amphibians, reptiles, birds and mammals), and selected data for humans. A partial list of the hearing functions included are: Auditory sensitivity and hearing range (audiograms), frequency and intensity discrimination, pitch and loudness estimation, all aspects of masking (including broad band noise, narrow band and tonal masking, non-simultaneous masking, psychophysical tuning curves, and auditory filter shape), temporal summation, temporal resolution, duration discrimination, echolocation acuity, amplitude modulation detection and discrimination, detection of electrical stimulation of the auditory nerve and brain, temporal pattern discrimination, hearing development, and all aspects of directional hearing.

Limitations

There are several reasons why a given data set might not be included in the book:

1) I may have missed relevant papers in my literature search. Since I plan to update this book in later editions, I would be most grateful to be notified of any omissions that may have occurred.

2) Any given reference may have presented so much data (e.g. many functions of frequency, or sensation level, many individual subjects' data, many parameters, etc.) that to include it all would have swollen the book well beyond its present size. In these cases, I have attempted to select representative functions or subjects, or I have averaged across parameters where no important experimental effects were apparent. In these cases, I have noted the existence of further data in the reference notes. Some psychometric functions are included as examples in different species, tasks, and conditioning paradigms, but the majority have not been included.

3) A given reference may not contain useful data in spite of a title that suggests otherwise. In some references, experiments were done and thresholds obtained, but the relevant data may not have been given. For example, some studies on the effects of trauma to the auditory system present changes in thresholds as a result of experimental manipulation, but not the control thresholds themselves.

4) In general, I have omitted thresholds obtained after lesions of the ear or auditory system. The focus of this book is on the data from normal auditory systems. In some cases, I have noted that a given lesion was made, and what the general finding was. I have left out most studies of temporary and permanent threshold shift due to ototoxicity and acoustic trauma; there are too many data. Perhaps another book like this one could focus on these. In a few cases, I have included acoustic trauma effects where the data are manageable and make important points about the mechanisms of normal hearing (e.g. for some of the non-mammals in which the functioning of the ear is not yet well understood, or for some mammals where the mechanisms of discrimination are revealed by the lesions).

5) I have omitted detailed reference to studies which demonstrate a

phenomenon (e.g. a learning curve or a discrimination ratio showing that a given discrimination is possible) but do not investigate it systematically, or obtain functional relationships. However, in some important cases, reference is made to the study without giving the data. In general, only psychophysical data are included in the book. This means that results in the form of "number of responses," or "number of animals responding," or discrimination ratios, etc, are left out. Exceptions to this can be found in the sections on the lateral line and amphibian hearing where so little data exist of any kind.

6) Data from a paper may not have been included here if, after several concerted efforts to make sense out of the paper and the data within it, I failed to do so.

7) Finally, I have attempted to include representative human thresholds for comparison with the non-human data, but have not attempted a complete review of the human literature. Again, there are too many data. In several cases, the human data included come from papers on animal psychophysics in which humans were tested in the same way.

Format of the Book

The book is organized by animal group (class), with the addition of a section on the lateral line system of fishes and amphibians. Each section begins with an Introduction and a Topical Index which functions as a Table of Contents. This index directs the reader's attention to the kinds of psychophysical data that exist for each animal group, and is designed to summarize each figure and table. The index is arranged alphabetically on major topics (e.g. frequency discrimination) but subordinate topics are arranged logically (as in the body of the book), rather than alphabetically. The idea is to make the Topical Index useful both as an index and as a Table of Contents. At the end of the book, the indices for each class section are combined, alphabetically, on major topic. This allows the reader to find everything on a major topic across animal groups. This combined index also functions as a snap-shot look at what aspects of vertebrate hearing have (or have not) been studied. In addition to the Topical Index, there is a Species Index (for common and scientific names) listing for each species the kinds of data available, Author Index, Bibliography, and Journal List.

Each class section begins with audiograms, and then continues with various studies of auditory detection and discrimination.

Record Format

The book is organized as a series of two-page mini-reviews, or records. Opening the book anywhere reveals a complete two-page record. The left page begins with a figure which plots the data in question. The figure is labeled with a capital letter (L,F,A,B,M, or C), referring to **lateral line**, **fish**, **amphibians-reptiles**, **birds**, **mammals**, or **comparative**, respectively, and a hyphenated number which indicates the sequence of figures. The label format (e.g. M6-0) is designed so that new records may be added in later editions (e.g M6-1) without the need to completely renumber the figures and tables.

All species are listed first by genus and species (italicized), and then by common name, as they have been presented by the authors of the papers referenced. Although this seems awkward and unnecessary for well-known species (e.g. cat, goldfish, and human), it is necessary for consistency in the context of so many different, and sometimes unfamiliar, species. The Species Index gives the scientific names for all common names, and vice versa. No systematic attempt was made to correct the authors in their use of common or scientific names.

Figure Format. An attempt was made to construct the figures in a standard way, for ease of interpretation and comparison across figures. (The figures were made using Symphony (Lotus Development), cleaned up and edited using Freelance Plus (Lotus Development), and laser printed (Hewlett-Packard Laser-Jet Plus) at 300 dpi on the top half of a page.) In most cases, logarithmic axes begin and end at integer powers of 10. Figures within a section which are useful to compare have the same axes with the same scale and dimensions. Sometimes this is awkward and leaves the data points crowded to one side or the other, but I believe that this is preferable to axis scales which change from figure to figure. The motivation is to facilitate comparisons across figures.

Each data set in a figure has its own symbol, and every symbol or line is coded with a number in the figure. The data corresponding to each symbol and number is briefly identified below the figure. At the bottom of the left page, the complete bibliographic references corresponding to all the data plotted are given in alphabetical order. This saves the reader from flipping back and forth to the combined bibliography at the end of the book to identify the complete reference of interest.

Table Format. On the right page, a table lists the coordinates of all the points plotted in the figure. The table columns are identified by the number used to code each symbol in the figure. The table numbers are those which were entered into the Symphony spreadsheet to create the figure. These numbers were taken from published tables in the original references, or were extracted from published figures. To obtain numbers from figures, I used a pair of good dividers and a millimeter rule. The errors arising using this procedure depended on the quality and size of the original figure, and my own eyeballing error (estimated to be about 0.2 mm). Great care was taken in reading numbers from the figures, but it is likely that some errors were made. I would most appreciate knowing about any errors that readers may find.

Note Format. Below the table are notes on various aspects of the data displayed in the figures and tables, identified by the appropriate number. The notes may include a mention of the conditioning and psychophysical method used, the number of subjects, the measure of central tendency used, any averaging or omission of data that I may have done, important details about the acoustic signals used, brief explanations or interpretations of the results (where appropriate or interesting), brief note of other results contained in the reference but not given in the figure and table, "see also" references to other records in the book, and citations of other relevant bibliographic references. These additional references are listed in the combined bibliography at the end of the book.

In some cases, the notes are lacking in some detail that the reader may

consider important. Often, this reflects the omission of details in the original reference. In some cases, however, certain details are omitted in order to keep to a two-page format. Each of these two-page records stands by itself to tell its story. However, the data presented in this book do not substitute for the original published papers. When it is critical to know the details of the methods and results from one of the references cited, the original paper should be read.

Conventions and Definitions

A number of formal conventions are used throughout the book for consistency and to promote intuitive understanding of the figures and tables. These conventions are noted here along with brief explanations and definitions of terms and concepts used throughout the book.

Frequency is given in Hz rather than kHz unless using the latter saves needed space in the text.

Sound pressure is given in dB re: 1 dyne cm^{-2} for all underwater conditions (fishes and marine mammals), and as dB SPL (sound pressure level) for all in-air conditions. Proper comparisons of hearing sensitivity in air and water are difficult to make. One common method of comparison is to express both air and water thresholds in units of **sound intensity** (e.g. in Watts cm^{-2}), which takes into consideration the impedance of the medium.

Note that:

0 dB SPL = 0.0002 dynes cm^{-2}

0.0002 dynes cm^{-2} is 20 micropascal, or 2×10^{-5} Pascal

1 Pascal = 1 Newton m^{-2}

1 dyne cm^{-2} = 0.1 Pascal

0.0002 dynes cm^{-2} is -73.98 dB re: 1 dyne cm^{-2}

In air, 0 dB SPL = 10^{-16} Watts cm^{-2}

In water, 1 dyne cm^{-2} = 6.8×10^{-13} Watts cm^{-2}

For equal intensity (in Watts), sound pressure in water is 35.6 dB above sound pressure in air.

Particle motion values are given in microns (micrometers) of displacement, or dB re: 1 micron. It is possible in many cases that the lateral line or auditory receptor responds in proportion to particle acceleration, however. Acceleration may be calculated by multiplying the displacement by $(2 \times \pi \times \text{frequency})^2$.

1 Angstrom = 10^{-10} meter.

Frequency discrimination thresholds are given as the frequency difference (in Hz) between two tones that are just discriminably different.

Intensity discrimination thresholds are given as the sound pressure difference (in dB) between two signals that are just discriminably different.

Sensation level (SL) refers to a level of a signal in dB relative to the signal level at absolute detection threshold.

Masking is defined as the reduction of the audibility of one sound caused by the introduction of another sound. In many studies of masker level, the signal threshold tends to rise one dB for every one dB increase in masker level. This means that the increment caused by adding the signal to the masker is constant in dB, (i.e., is a constant proportion of masker sound pressure). This is equivalent to **Weber's Law** which states that a just-detectable increment in stimulus intensity is a constant proportion of the base intensity.

Forward masking refers to a case in which the signal to be detected is presented after the masker stimulus has ended. This is a way to probe the persistence of the effect of the masker in the auditory system. The locus of the persisting effect is likely at the synapse between hair cells and auditory nerve fibers.

Backward masking refers to the case in which the signal to be detected begins and ends before the masker stimulus has begun. The locus of this masking effect is likely more central than that for forward masking.

Simultaneous masking refers to the case in which the signal to be detected is presented during the masker.

Critical masking ratio, or CR (signal-to-noise ratio at threshold) is the decibel difference between the sound pressure level of the signal tone at threshold and the spectrum level of the masking noise in the frequency region of the signal. **Spectrum level** is the sound pressure level of the noise within a one Hz-wide band. This can be calculated from a pressure level (in dB) in a wider band (B Hz wide) by subtracting $10\log_{10}(B)$ from the pressure level. Equivalent "critical ratio bandwidths" in Hz can be calculated as $10^{(CR/10)}$.

Critical bandwidth is the frequency range (in Hz) within which the intensity of a stimulus summates over frequency in its effect on the auditory system. Most often, the "effect" measured is the masking effect of a noise band on the detection of a tone centered (in frequency) in the band.

Psychophysical tuning curves (PTC) are measures of the frequency selectivity of a filtering system. They are usually obtained by determining the level of a masker (often a tone) required to just mask a tone or narrow noise band signal (fixed in level near absolute threshold) as a function of the masker frequency. This procedure presumably results in the measurement of the frequency selectivity of a small number of channels having center frequencies near the signal frequency.

Q_{10dB} is a relative measure of the frequency selectivity (tuning) of a filtering system. It is calculated as the center frequency of the filter (in Hz) divided by the bandwidth (in Hz) at levels 10 dB above best sensitivity.

Binaural masking level difference (BMLD) is a phenomenon of binaural hearing in which there is a release from masking under conditions producing different interaural relations (e.g. interaural differences in phase or intensity) for the signal and for the masker. For example, if a tone and

noise masker are identical in waveform at both ears (diotic, or N_oS_o), the masking effect is greatest. If the signal is then simply inverted in polarity in one ear relative to the other (N_oS_{pi}), the masking effect is reduced by several dB (i.e., the signal is more detectable). This effect is probably best viewed as an adaptation for directional filtering, since such interaural differences would arise if the signal and masker sources were located at different azimuths. The BMLD is one way to define the "cocktail party effect."

Amplitude modulation. For amplitude modulated signals, the modulation depth is indicated by m which is equal to $(P-T)/(P+T)$, where P is the sound pressure at an envelope maximum and T is the sound pressure at a minimum. This value varies between zero and one; one indicating 100% modulation. The value m is usually scaled as $-20 \log_{10}(m)$ so as to expand the scale at low modulation depths. For sinusoidal amplitude modulation (SAM), $20 \log_{10}(m)$ is the attenuation of the side bands (in dB) relative to the 100% modulated case.

Amplitude modulated noise is used to measure the "**temporal modulation transfer function**" (TMTF). This is defined as the smallest modulation depth that still allows the animal to discriminate between modulated and unmodulated noise, determined at a number of modulation rates. The resulting function can be thought of as the frequency response of an hypothetical internal low-pass filter through which envelope fluctuations pass, and which limits the effective modulation depth of the internal (physiological) representation of the envelope.

Amplitude modulated signals are also used to measure the temporal resolution of the auditory system in representing and processing the time structure of the modulated envelope. In this case, animals are asked to discriminate between different modulation rates. Such thresholds can also be thought of as estimates of the animal's ability to measure the time interval between successive peaks in the envelope, and may be similar to duration discrimination thresholds.

Temporal summation. In studies of temporal summation at threshold, perfect summation or integration of sound intensity (energy detection) occurs when a 10-fold increase in sound duration results in a 10 dB (intensity factor of 10) reduction of sound pressure at threshold.

Repetition noise is a stimulus created by splitting the output from one noise source into two channels, and then adding them together after delaying and attenuating one of the channels. This produces a noise whose amplitude spectrum is a sinusoidal function of frequency, and which has a peak in the autocorrelation function at the delay time (T sec). The autocorrelation peak indicates an essential periodicity in the noise fine structure caused by adding back a delayed version of the original noise (as an echo). The first peak of the spectrum above zero Hz occurs at $1/T$ (in Hz), and all subsequent peaks are spaced by $1/T$ Hz. Humans perceive this stimulus to have a pitch equal to a pure tone of $1/T$ Hz. The pitch could arise either from an

autocorrelation-like process (time domain analysis) or a filter bank-like process (frequency domain analysis), and the interesting question concerns which of these the auditory system uses. Attenuating the delayed channel reduces the spectral modulation depth (peak-to-trough differences across the frequency spectrum).

If the delayed channel of repetition noise is inverted before adding - producing "cos-" noise - an autocorrelation null appears at the delay time, and the first trough of the spectrum occurs at $1/T$ Hz. This produces a slightly weaker and ambiguous pitch for human observers.

Minimum audible angle (MAA) refers to the smallest angular difference between two sound sources that allows the observer to discriminate the difference between successive sounds from one source location and successive sounds from different source locations.

Conditioning and Psychophysical Methods

In the notes for each record, I briefly describe the conditioning procedures used. I have attempted to use the terminology and spelling conventions of the authors of the papers referenced in this description.

Instrumental avoidance conditioning refers to cases in which the animal is trained to perform a response (e.g. crossing a barrier, lifting a paw, licking a tube) in order to avoid shock or other noxious stimulus. The auditory signal in the experiment signals impending shock, and the criterion response is used to indicate hearing or discrimination, and causes the shock to be omitted.

Operant conditioning for reward (usually food or water) refers to cases in which the animal is trained to emit a criterion response (e.g. press a lever, nose a panel, or move to a certain location) in the presence of an auditory signal in order to receive the reward. The motivation is hunger or thirst. A response in the presence of the signal is used to indicate hearing or discrimination, and results in reward. Often, operant paradigms chain several responses in order to control the position of the animal in the sound field. In many cases, the animal can initiate a trial by emitting an "observing response". This helps ensure that the animal is ready to listen. Then a signal is presented following a random time delay from the observing response, and a second response within a criterion time from signal onset is used to indicate hearing or discrimination, and results in reward.

Classical (Pavlovian) conditioning refers to the case in which a stimulus (often shock) produces a reflex response (e.g. respiratory or cardiac suppression). The shock is termed the unconditioned stimulus (UCS) and the reflex is termed the unconditioned response (UCR). In delay conditioning, an auditory signal is presented for several seconds prior to the UCS and can be thought of as a signal for the impending UCS. After several pairings of the signal and the UCS, the signal comes to elicit a response often similar to the UCR. At this point, the signal is termed a conditioned stimulus (CS) and the response to it is termed the conditioned

response (CR). The CR is used to indicate hearing or discrimination.

Conditioned suppression is a combination of operant and classical conditioning. The animal is trained to emit a steady stream of responses (e.g. pressing a bar or licking a tube) for a reward which is intermittently given. Then a shock (or other noxious stimulus) is introduced (the UCS) which interrupts the operant response stream. An auditory signal precedes the UCS and becomes a CS after several UCS-CS pairings. The interruption of the operant behavior stream is the CR and is used to indicate hearing or discrimination.

Psychophysical Methods

There are many psychophysical methods and variants used to measure thresholds, and many definitions of threshold used in the literature reviewed. The following are brief descriptions of those most often used.

The method of limits is a classical psychophysical procedure in which the magnitude of a stimulus (sound intensity or the size of the difference between two stimuli that are to be discriminated) is reduced on successive trials from a level producing a clear behavioral response to one that does not. A second series then begins with the stimulus ascending in level. These series may be alternated several times. Threshold is defined as the averaged stimulus level half way between levels which result in a response to the signal and levels which do not. Often a "modified" method of limits is used. In these cases, only the descending or ascending series may be run. Sometimes a blocked method of limits is used in which several trials are presented at the same stimulus level before the level is changed.

The staircase procedure is another variant of the method of limits and may be identified by some authors as a modified method of limits. In this case, signal level is reduced toward threshold in steps (the size of which may vary) until a "no-response" criterion is reached. The level then begins to increase until the response criterion is reached, and then decreases again. The averaged signal levels at the transitions between response and no-response are defined as threshold. This is an efficient procedure but sometimes fails because the signal levels are constantly very near threshold.

The staircase procedure and its variants are often termed tracking, adaptive tracking, or adaptive procedures. Sometimes two positive responses in a row at the same signal level are required before the signal level is reduced (known as the two-down, one-up rule). In a two-alternative forced choice paradigm, the threshold converges on about 71% correct. In some cases, the tracking procedure continues until some running statistical criterion for stability is reached.

The method of constant stimuli is a classical procedure in which blocks of trials are presented, all at the same signal level. A "percent correct" is calculated for the given signal level, and a new block begins at a different signal level. Several levels are chosen to "bracket" the suspected threshold. Percent correct plotted as a function of signal level produces the psychometric function, and a threshold may be defined as the

interpolated signal level corresponding to some percent correct value. In a "yes-no" or "go, no-go" paradigm (in which the animal either responds or does not on a given trial), a value near 50 percent correct defines the threshold. In a "two-alternative forced-choice" paradigm (in which the animal responds on every trial with one response or another, such as "go-right or go-left"), a value near 75 percent correct may define the threshold.

In sophisticated psychophysical paradigms, analyses of errors as well as correct responses can be usefully made. Errors are "false alarms" (responding "yes" when the signal was not present) and "misses" (responding "no" in the presence of a signal). Correct responses are "hits" (correctly detecting the signal) and "correct rejections" (responding "no" when the signal was not presented). With such measures, response bias (such as an overall tendency to say "yes" in a "yes-no" task) can be measured and overall performance measures such as d' can be obtained that are free of the effects of bias.

Some of the data presented in this book are obtained from stimulus generalization experiments, and are thus not strictly psychophysical data. In this type of experiment, animals are trained to respond to a given stimulus, and then tested for response to other stimuli that differ from the training stimulus along one or more physical dimensions. The value of this kind of measure is that it helps to show what dimensions of the stimulus control behavior, or are salient to the animal.

Lateral Line System

The lateral line system of fishes and some aquatic (and some larval) amphibians consists of patches of sensory tissue (maculae) composed of hair cells and support cells covered with gelatinous cupulae. These are known as neuromasts and are found "free" on the body and head, and in canals on the head and trunk. The trunk and head "line" of neuromasts open to the water environment through pores. The pores and associated pigmentation are often recognizable to the eye as a stripe along the side of the body. The head canal system and its pores are less easily seen. There is considerable variation among species in the types and distribution patterns of lateral line organs.

Lateral line receptor cells (the hair cells) respond to displacement of the cupula. Cupular displacement results ultimately from a relative movement between the animal's skin and the surrounding water. Because of the complexity of the hydrodynamics intervening between the relative water/skin movement and the receptor cells, receptor displacement is proportional to water particle acceleration in many systems. However, responses proportional to water particle velocity or displacement may occur in some systems. In some surface-feeding fishes and amphibians, neuromast organs near the water surface detect surface waves as well as underwater waves.

Formerly, the lateral line system was viewed by some as closely associated with the auditory system in function, and some have referred to it as an "accessory hearing" organ. More recently, the lateral line system has been viewed on its own terms (as originally suggested by Dijkgraaf, 1964) as a mechanoreceptor system responsive to low frequency hydrodynamic fields (for example, as produced by nearby swimming fishes or prey). Its effective range appears to be from millimeters to a body length or two. The lateral line system does not respond to sound pressure, or to far-field acoustic particle motion where the spatial gradient of motion amplitude is very shallow (in which case the fish and surrounding water move together and no relative motion occurs). The lateral line may respond in the near field of sound sources (in which case there is a significant gradient of hydrodynamic motion amplitude over the animal's body).

Very little is known about the sensitivity and discriminative capacities of animals based on input to the lateral line system, as the brevity of this section suggests. In general, however, it now seems that its sensitivity is similar to the auditory system of fishes and other vertebrates in a frequency range from about 10 to several hundred Hz (Fig. L1-0). Wave frequency discrimination is possible (from 4 to 10%; Fig. L3-0) and is presumably based on processing temporally coded information. The lateral line system is directionally sensitive and allows a determination of source location (and distance) in some cases, at least (Figs. L4-0 and L6-0). The wide spatial distribution of the neuromast organs suggests that an important function of the lateral line system is in detecting and discriminating the spatial characteristics of hydrodynamic fields. Little is known about the capabilities of the system for spatial analysis (see Fig.

L7-0).

See Coombs, Janssen, and Webb (1988) and Denton and Gray (1988), for reviews of lateral line system morphology, biophysics, and physiology.

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Lateral Line System

Detection sensitivity

In three species L1-0

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Presumed lateral line sensitivity in two species L2-0

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Reaction time as a function of stimulus frequency L5-0

Texture discrimination (spatial frequency analysis) L7-0

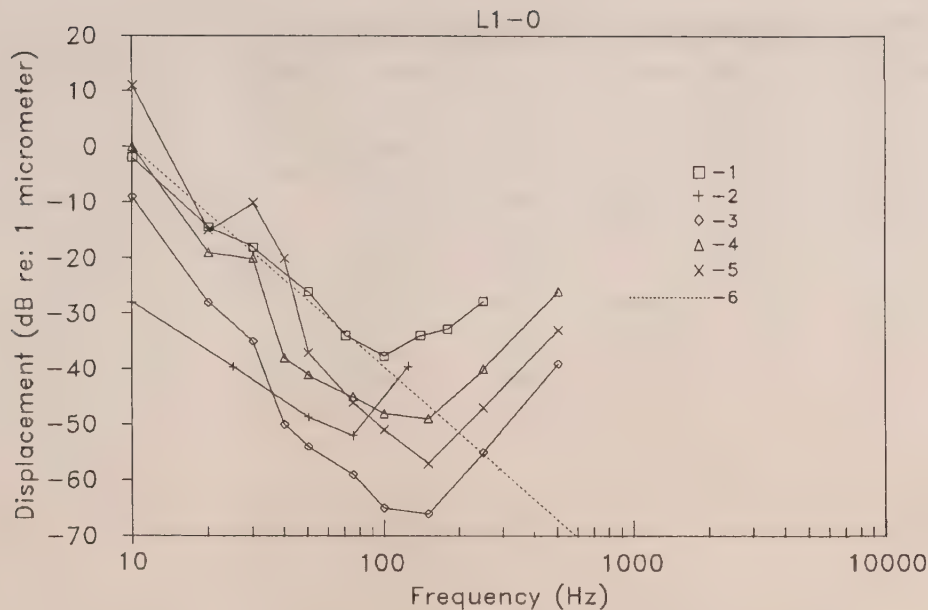


Fig. L1-0. Lateral line detection thresholds for three fish species.

- 1- *Aplocheilus lineatus* - a topminnow (Bleckmann, 1980)
- 2- *Acerina cernua* - ruff (Kuiper, 1967)
- 3- *Cottus bairdi* - mottled sculpin, head (Coombs and Janssen, 1988)
- 4- *Cottus bairdi* - mottled sculpin, trunk (Coombs and Janssen, 1988)
- 5- *Cottus bairdi* - mottled sculpin, tail (Coombs and Janssen, 1988)
- 6- Acceleration = -50 dB re: 1 meter sec⁻²

References:

- Bleckmann, H. (1980) Reaction time and stimulus frequency in prey localization in the surface feeding fish, *Aplocheilus lineatus*. *J. Comp. Physiol.* 140, 163-172.
- Coombs, S.C. and Janssen, J. (1988) Peripheral processing by the lateral line system of the mottled sculpin. In S. Coombs, P. Gorner, and H. Munz (eds), *Neurobiology and Evolution of the Lateral Line System*. Springer-Verlag: New York.
- Kuiper, J.W. (1967) Frequency characteristics and functional significance of the lateral line organ. In P.H. Cahn (ed), *Lateral Line Detectors*. Indiana University Press: Bloomington, pp. 105-121.

Table L1-0. Lateral line detection thresholds for three fish species.

Frequency (Hz)	Displacement (dB re: 1 micrometer), or relative*				
	1	2	3	4	5
10	-1.9	-28	-9	0	11
20	-14.4		-28	-19	-15
25		-39.6			
30	-18.1		-35	-20	-10
40			-50	-38	-20
50	-26	-48.7	-54	-41	-37
70	-34				
75		-52	-59	-45	-46
100	-37.7		-65	-48	-51
125		-39.5			
150			-66	-49	-57
140	-34				
180	-32.8				
200		-43			
250	-27.7		-55	-40	-47
500			-39	-26	-33

Notes:

It has become clear that most lateral line organs respond to the acceleration of the water relative to the fish's skin, and in this case it might be best to show these thresholds in terms of water particle acceleration. However, the displacement parameter is more intuitive to most people, so the data are plotted as displacement thresholds. The dashed line connects points of equal particle acceleration (about -50 dB re: 1 meter sec⁻²) to give an acceleration reference in the figure. Compare these data with displacement sensitivity of the auditory system in Fig. F15-0.

1- This is a surface-feeding fish which uses lateral line organs on the head (positioned at the water surface) to detect, identify, and locate the sources of surface disturbances. Threshold in dB re: 1 micron vertical displacement of water surface waves. Orienting response to surface waves. Means: N=2.

*2- In this species the side line component of the lateral line system was tested. Stimulus was produced by implanting magnets on the animal's skin and manipulating a magnetic field. Threshold in dB re: displacement sensitivity at 75 Hz (estimated by the author as about 25 Angstroms). Conditioned feeding response.

3-5- This is a bottom-dwelling fish from Lake Michigan. Unconditioned turning and snapping response to the onset of a sinusoidal signal produced within one cm of the fish by a vibrating sphere (dipole). Tracking psychophysical method. Signal levels were measured by an hot-wire anemometer (measuring hydrodynamic particle velocity) replacing the fish in the apparatus. Data sets #3, #4, and #5 were obtained with the stimulus near the head, middle trunk, and tail region, respectively. The head region shows the greatest lateral line sensitivity and the tail the least. Means: N=3.

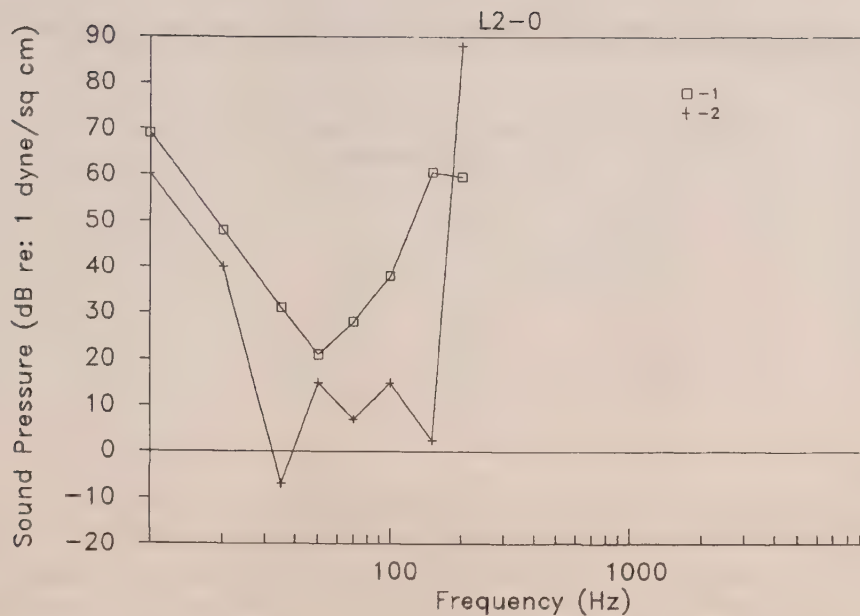


Fig. L2-0. Detection thresholds for two fish species presumed to be mediated by the lateral line system.

- 1- *Carassius auratus* - goldfish (Weiss, 1969)
- 2- *Anoptichthys jordani* - blind cavefish (Weiss and Martini, 1970)

References:

- Weiss, B.A. (1969) Lateral-line sensitivity in the goldfish (*Carassius auratus*). J. Aud. Res. 9, 71-75.
- Weiss, B.A. and Martini, J.L. (1970) Lateral-line sensitivity in the blind cavefish (*Anoptichthys jordani*). J. Comp. Physiol. Psychol. 71, 34-37.

Table L2-0. Detection thresholds for two fish species presumed to be mediated by the lateral line system.

Frequency (Hz)	Sound Pressure Threshold dB re: 1 dyne cm ⁻²	
	1	2
10	69	60
20	48	40
35	31	-7
50	21	15
70	28	7
100	38	15
150	60.5	2.5
200	59.5	88

Notes:

Instrumental shock avoidance (barrier crossing) using the single staircase psychophysical procedure with 5 dB step size. Means: N=5 *C. auratus*, N=3 *A. jordani*.

The methods and procedures were essentially identical for both studies, and for the studies on hearing in *C. auratus* (Fig. F1-0, Weiss, 1966) and *I. nebulosus* (Fig. F2-0, Weiss, Strother and Hartig, 1969). The rationale for these being lateral line system thresholds is essentially that training was begun at very low frequencies where the lateral line is presumed to be relatively more sensitive than the ear. The authors believe that once trained to use the lateral line for detection, there is little generalization to the use of the ears at frequencies where the ears are presumed to have comparable sensitivity. Compare these functions with those for the same species presumably detecting sound using the ears (Figs. F1-0 and F4-0).

The sound field was produced between facing J9 projectors operating 180° out of phase. This unusual arrangement was created to produce a uniform sound field. The sound signal likely had a large displacement component relative to the pressure component. However, since it is also likely that the water mass (and the fish being tested) were accelerated uniformly, there would have been little relative movement between the fish and the water, and thus little lateral line stimulation. At the same time, there would likely be efficient stimulation of the vestibular system (particularly the utricle and lagena in these species). There was no measure of acoustic particle motion.

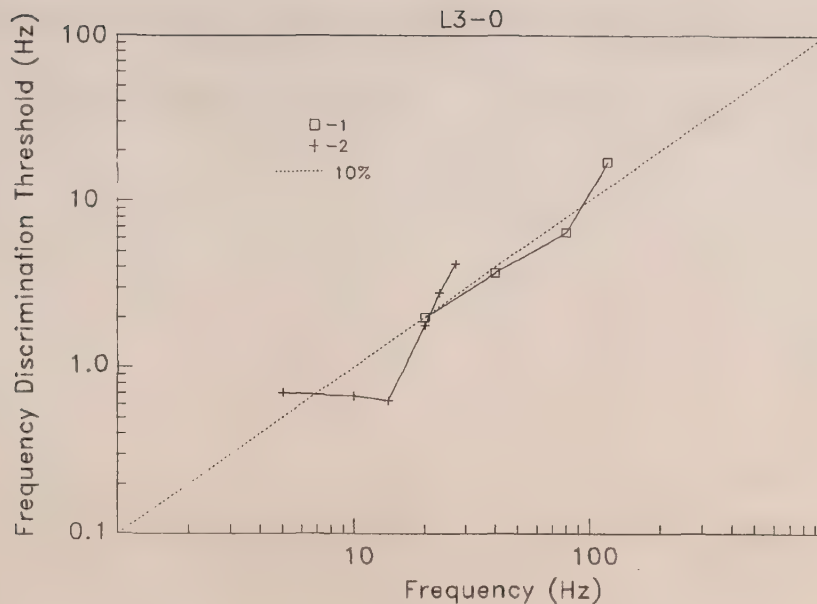


Fig. L3-0. Frequency discrimination thresholds for the lateral line system of fishes and an aquatic frog.

- 1- *Aplocheilus lineatus* - topminnow (Bleckmann, Waldner, and Schwartz, 1981)
- 2- *Xenopus laevis* - African clawed toad (Elepfandt, Seiler, and Aicher, 1985)
- 3- Discrimination threshold of 10%

References:

- Bleckmann, H., Waldner, I., and Schwartz, E. (1981) Frequency discrimination of the surface-feeding fish *Aplocheilus lineatus* -- a prerequisite for prey localization? J. Comp. Physiol. 143, 485-490.
- Elepfandt, A., Seiler, B., and Aicher, B. (1985) Water wave frequency discrimination in the clawed frog, *Xenopus laevis*. J. Comp. Physiol. 157, 255-261.

Table L3-0. Frequency discrimination thresholds for the lateral line system of fishes and an aquatic frog.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)	
	1	2
5		0.7
10		0.67
14		0.63
20	2	1.8
23		2.8
27		4.2
40	3.7	
80	6.5	
120	17.2	

Notes:

It is likely that the ability to perform frequency discrimination using the lateral line system is based on the coding and analysis of the stimulus waveform in the time domain. These two studies on different species show relative thresholds averaging about 10%. Note that Elepfandt (1986) has also shown that the African clawed toad is capable of a recognition and memory for the absolute frequency of water waves.

1- This is a surface-feeding fish. Stimuli were 750 msec sinusoidal water surface waves. Conditioned differential discrimination, approach and snapping for food. Blocked descending method of limits psychophysical procedure.

2- Stimuli were 3 sec duration sinusoids produced by vibration of a 2 cm diam cylindrical probe, extended 2 mm below water surface. Conditioned differential discrimination, defined by the animal's orientation to the stimulus. Blocked descending method of limits psychophysical procedure. The authors noted that frequency discrimination occurred in detecting both surface waves and underwater waves. Means: N=3.

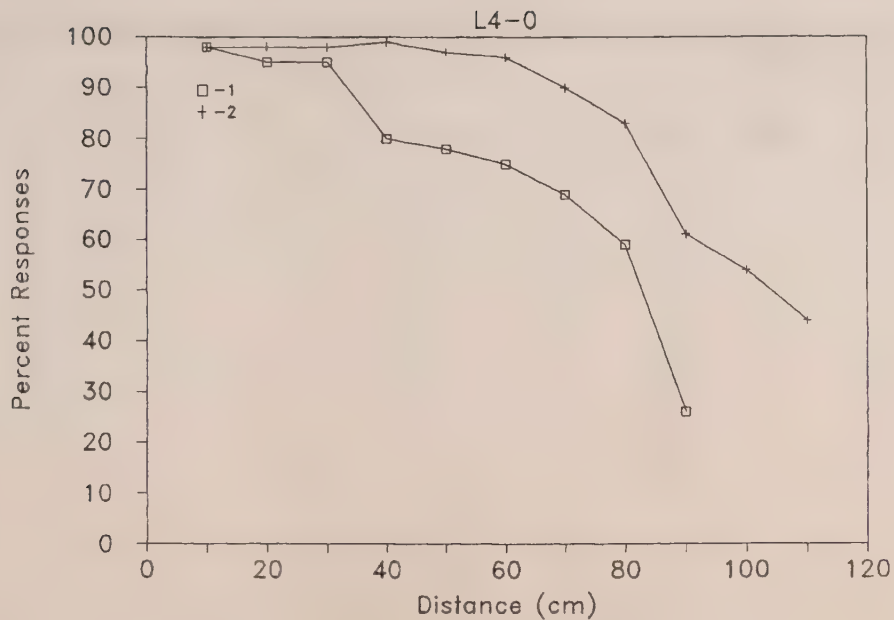


Fig. L4-0. The responsiveness of two fish species to water surface waves as a function of source distance (Schwartz, 1967).

- 1- *Fundulus notatus* - a topminnow
- 2- *Aplocheilichthys lineatus* - a topminnow

Reference:

Schwartz, E. (1967) Analysis of surface-wave perception in some teleosts. In P.H. Cahn (ed), Lateral Line Detectors. Indiana University Press; Bloomington, pp. 123-134.

Table L4-0. The responsiveness of two fish species to water surface waves as a function of source distance.

Source Distance (cm)	% Response	
	1	2
10	98	98
20	95	98
30	95	98
40	80	99
50	78	97
60	75	96
70	69	90
80	59	83
90	26	61
100	54	
110	44	

Notes:

These distance data are rather arbitrary measures of lateral line performance since the distance at which the animals detect the signal will likely depend on the amplitude of the signal as well. Here, the signal amplitude was adjusted to be approximately equally detectable in each species so that the difference between the curves could reflect a species difference in responding to sources at different distances.

Orienting response of surface-feeding fish to water surface waves. Waves produced by dipping a glass rod into the water. Each point based on 384 trials. Means: N=7.

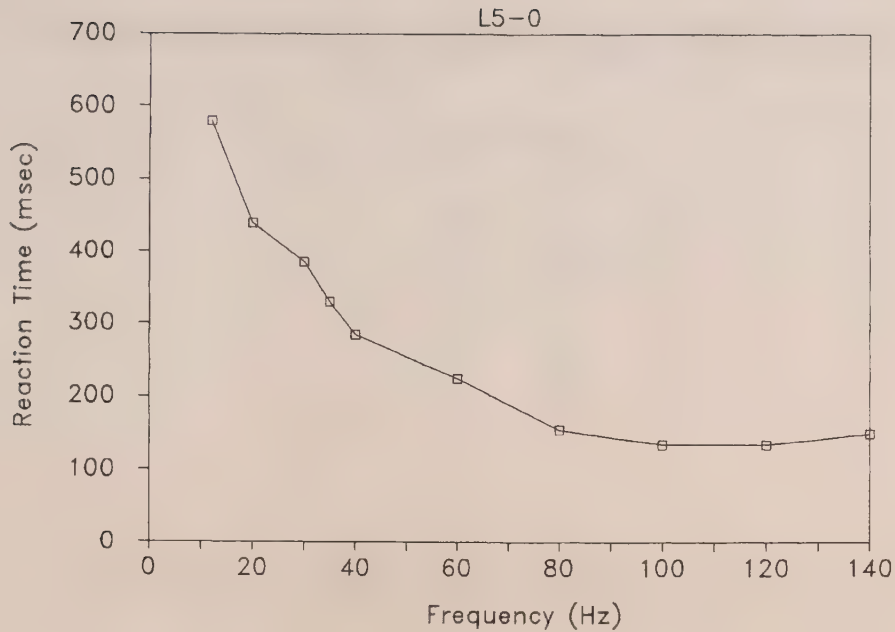


Fig. L5-0. Reaction time to water surface waves as a function of wave frequency in *Aplocheilus lineatus* (a topminnow) (Bleckmann, 1980).

Reference:

Bleckmann, H. (1980) Reaction time and stimulus frequency in prey localization in the surface feeding fish, *Aplocheilus lineatus*. J. Comp. Physiol. 140, 163-172.

Table L5-0. Reaction time to water surface waves as a function of wave frequency in *Aplocheilichthys lineatus* (a topminnow) (Bleckmann, 1980).

Frequency (Hz)	Reaction Time (msec)
12	580
20	440
30	385
35	330
40	285
60	225
80	155
100	135
120	135
140	150

Notes:

Waves produced by vibrating 4 mm diam. probe at water surface. Duration approximately 700 msec. Vertical displacement amplitude approximately 2 microns. The authors note that this function indicates that about 8.4 wave cycles are required for a response, regardless of the wave frequency. Based on 333 responses.

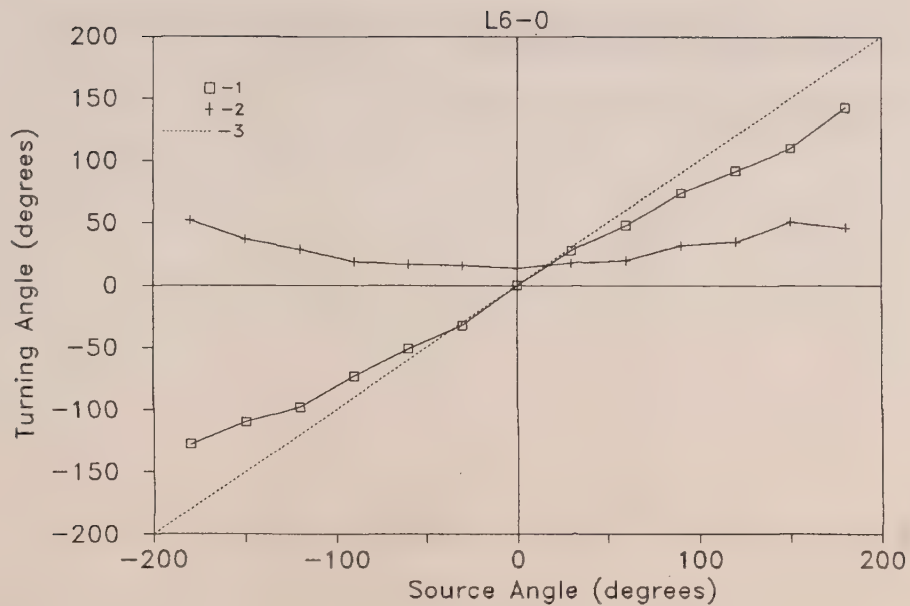


Fig. L6-0. Azimuthal localization of water surface waves by *Xenopus laevis* (African clawed toad) (Gorner, et al, 1984).

- 1- Means
- 2- Standard Deviations
- 3- Perfect Localization Performance

Reference:

Gorner, P., Moller, P. and Weber, W. (1984) Lateral line input and stimulus localization in the African clawed toad, *Xenopus* sp. J. Exp. Biol. 108, 315-328.

Table L6-0. Azimuthal localization of water surface waves by *Xenopus laevis* (African clawed toad) (Gerner, et al, 1984).

Stimulus Angle (degrees)	Response Angle (degrees)	
	1	2
-180	-128	52
-150	-110	37
-120	-98	29
-90	-73	19
-60	-51	17
-30	-32	16
0	0	14
30	28	18
60	48	20
90	74	32
120	92	35
150	110	51
180	143	46

Notes:

The stimulus was a water surface wave produced by a drop of water falling from 13.5 cm to the water surface. In this task, the animal was presented with a source at a given azimuth, causing an unconditioned orienting response. The orientation of the animal following the response was measured. Means: N=9.

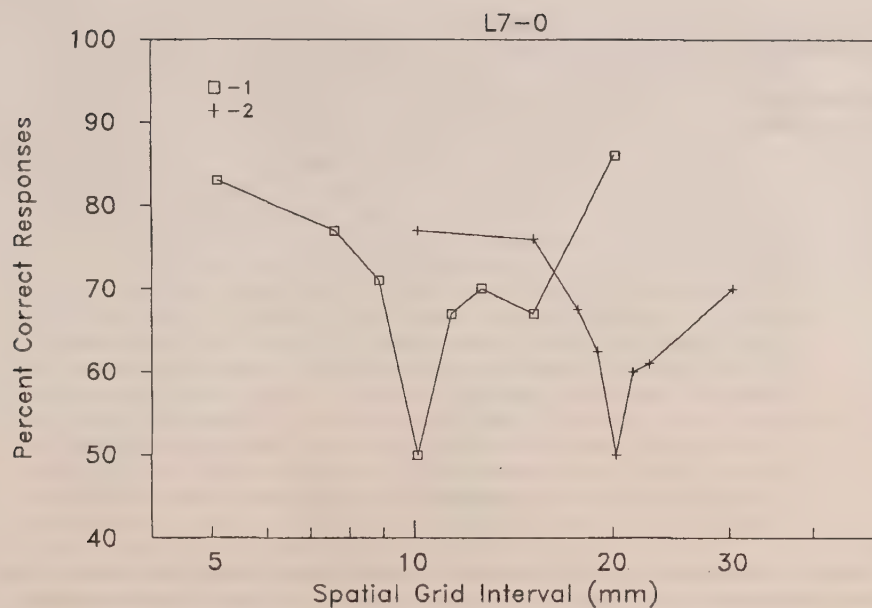


Fig. L7-0. Spatial interval discrimination by the lateral line system of *Anoptichthys jordani* (blind cave fish) (Hassan, 1986).

1- 10 mm interval standard stimulus
 2- 20 mm interval standard stimulus

Reference:

Hassan, E. (1986) On the discrimination of spatial intervals by the blind cave fish (*Anoptichthys jordani*). J. Comp. Physiol. 159, 701-710.

Table L7-0. Spatial interval discrimination by the lateral line system of *Anoptichthys jordani* (blind cave fish) (Hassan, 1986).

Comparison Stimulus Interval (mm)	Percent Correct Responses	
	1	2
5	83	
7.5	77	
8.75	71	
10	50	77
11.25	67	
12.5	70	
15	67	76
17.5		67.5
18.75		62.5
20	86	50
21.25		60
22.5		61
30		70

Notes:

Animals were trained for a food reward to discriminate between grid panels having different grid spacings. The grid panels were made up of 1 mm diam vertical rods fixed with a particular periodic spatial interval to a plastic plate. On a given trial, the experimental test tank was divided by two grid panels placed side-by-side, each with a door opening allowing access to the other half of the tank. One panel was the "standard" grid (either 10 or 20 mm spatial interval), and the other was the "comparison" grid, with a wide range of possible spatial intervals (see Table above). The animal was rewarded for passing through the door on the "standard" grid side. The fish typically swam past the grids before making a discriminative response. The difference in spatial interval was successively reduced and the percent correct responses recorded. Each point plotted above was based on at least 400 responses. The results show that the fish can detect spatial interval differences of between 7.5 and 15% (1.5 mm in the context of 10 and 20 mm standard intervals). Means: N=2.

This highly original experiment shows that the mechanoreceptive lateral line system can be used to actively explore the spatial textures of the environment.

Hearing in Fishes

The auditory organs of fishes are otolith organs (sacculus, lagena, and utricle) composed of a patch of sensory tissue containing hair cells and support cells overlain by a dense, solid, calcium carbonate otolith. In sharks and other elasmobranchs, the "otolith" is a sac full of a slurry of otoconial crystals. The otolith organ most used in hearing varies among species. In the herrings, the utricle is specially adapted for receiving acoustic input. In most fishes, the sacculus is the primary auditory organ. The function of the lagena in hearing is not understood. All otolith organs are sensitive seismic detectors with the sacculus and lagena "looking" primarily in the vertical plane, and the utricle "looking" horizontally.

The adequate stimulus at the receptor level is displacement of the hair cell stereocilia, which can occur several ways. In the most general case, the otolith organs appear to function as mass-loaded accelerometers, responding to acceleration of the head. The fish's body tissues are similar in acoustic impedance to the surrounding water. Therefore, sound impinging on the fish is transmitted through the body, and acoustic particle motion brings the fish's body into motion. This is detected as a relative motion between the otoliths and the hair cell stereocilia due to the tendency of the otolith to move at a different amplitude and phase than other tissue. The hair cells are thus stimulated inertially by particle acceleration.

Most fishes have a swimbladder or other gas-filled "bubble" in the abdominal cavity or head. As sound pressure fluctuations occur, the bubble expands and contracts according to the amplitude of motion characteristic of the enclosed gas. The swimbladder thus becomes a monopole sound source. The motions of the swimbladder walls may reach the ears of some species, and cause fluid motion that results in a relative motion between the otoliths and underlying hair cells. In this case, the sound pressure amplitude determines hair cell stimulation. In most fishes, response of the ear to sound is determined simultaneously by the ear detecting particle motion in its "accelerometer" mode, and by the ear detecting sound pressure via the swimbladder response. The swimbladder is well damped, and its motion tends to be independent of frequency in the frequency range of hearing. Thus, the contribution of the swimbladder to hearing grows at higher frequencies.

In some species, the swimbladder is specifically linked to the ear via specialized mechanical pathways. The best known such pathway is the Weberian ossicle system; a series of four bones connecting the anterior swimbladder wall to the ears. Fishes with such ossicles are known as Ostariophysi or Otophysi, and are considered to be "hearing specialists" in that their sensitivity and bandwidth of hearing is generally greater than for animals lacking such a system. The herrings and the mormyrids have gas bubbles near the ears in the head and are thus also considered to be "hearing specialists." Other specialists include those species in which extensions of the abdominal swimbladder project forward toward the ears.

The large amount of auditory psychophysical data on the fishes has helped to establish the notion that fishes have true vertebrate auditory systems, and hear in the same sense that other vertebrates hear. Such a conclusion is only possible to form on the basis of behavioral studies of their sensitivity and discriminative acuity for sound. Most all published

data on this question can be found in the 61 figures and tables to follow. Reviews of the anatomy and physiology of fish auditory systems can be found in Fay (1981), Platt and Popper (1981), and McCormick and Braford (1988).

Figs. F1-0 - F18-0 show hearing sensitivity data (audiograms). Best sensitivity for hearing specialists is -40 to -50 dB, between 200 and 1500 Hz. A useful range of hearing for these species can be defined as from below 100 Hz to about 2000 Hz. Fishes without swimbladders or without clear connections between the swimbladder and the ear have best sensitivities between -35 and about 10 dB, between 50 and 500 Hz. Sound pressure thresholds for fishes which do not use the swimbladder in hearing are inadequate descriptors of sensitivity. The sensitivity of these animals is thus dependent on sound source distance (F18-0), and is better described in terms of acoustic particle motion (F14-0, F15-0).

There is controversy in the literature on intensity discrimination sensitivity (F19-0). Best differential sensitivity ranges between about 1.3 dB to 4 dB. The intensity discrimination threshold (in dB) is nearly independent of signal level (F20-0) in accord with Weber's Law. Intensity discrimination for pulsed tones depends on signal duration (F21-0) in much the same way that signal detection depends on duration (F50-0 to F54-0), although there is controversy on this duration dependence for detection.

Critical masking ratios (CR) generally grow with signal frequency at about 3 dB per octave, indicating constant Q auditory filters with bandwidths slightly wider than for other vertebrates (F22-0, F23-0). The CR varies with the angular separation of signal and masker (F24-0, F25-0) indicating directional hearing and directional filtering. Critical bandwidths (F26-0) have been demonstrated in fishes as in other vertebrates.

Auditory filter shapes have been described using several methods (F27-0 to F35-0), and are qualitatively like those observed in other vertebrates. Forward masked psychophysical tuning curves (PTC) are not necessarily more sharply tuned than simultaneously masked PTCs (F30-0, F34-0). PTCs often show sharper tuning than peripheral nerve fibers (F36-0) for reasons that are not yet clear. Frequency selectivity has been demonstrated using threshold shifts following intense tone stimulation (F37-0).

Frequency discrimination thresholds increase proportionally with frequency, ranging from 3 to about 10% (F38-0 to F39-0). Data sufficient to reveal clear species differences. Tone frequency seen onto a monotonic perceptual dimension similar to "pitch" (F40-0). good evidence that frequency discrimination and other aspects of quality analysis is accomplished by processing the time structure stimulus directly, as is also the case for the lateral line system.

The fish auditory system is well able to process sound amplitude fluctuations, both with respect to sensitivity (F43-0, F44-0, F45-pattern discrimination (F46-0, F47-0AB, F48-0).

Forward, backward, and simultaneous masking phenomena are similar to those phenomena in other vertebrates (F49-0, F60-0).

Repetition noise (echo) processing in fishes (F55-0 to F59-0) is similar to that observed in man, and is likely the result of time-domain neural processing.

Fishes can discriminate sound source location in azimuth and elevation (F61-0) with an accuracy characteristic of other vertebrates.

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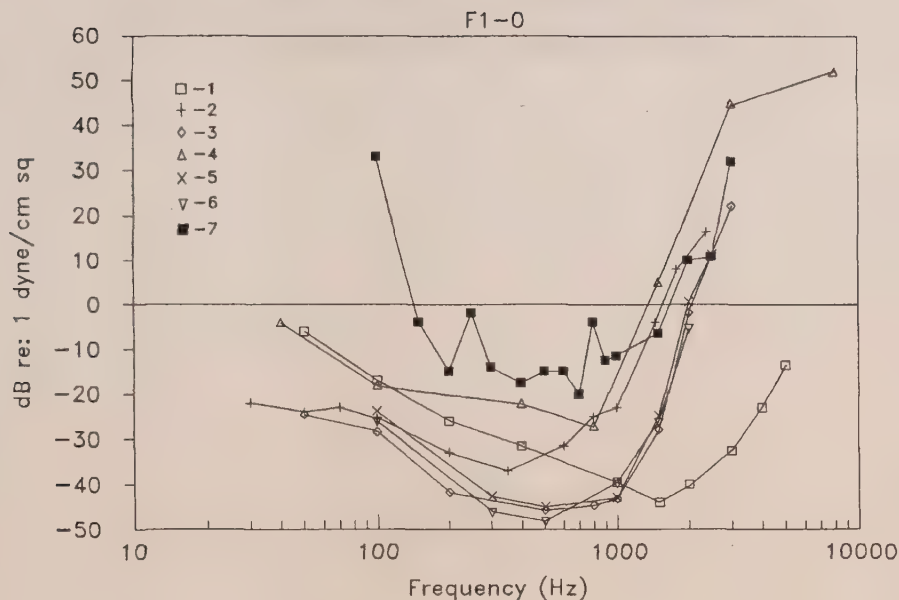


Fig. F1-0. Sound pressure audiograms for *Carassius auratus* (goldfish).

- 1- Enger, 1966
- 2- Fay, 1969b
- 3- Jacobs and Tavalga, 1967
- 4- Offutt, 1968
- 5- Popper, 1971 (45-48 mm fish)
- 6- Popper, 1971 (110-120 mm fish)
- 7- Weiss, 1966

References:

- Enger, P.S. (1966) Acoustic threshold in goldfish and its relation to the sound source distance. *Comp. Biochem. Physiol.* 18, 859-868.
- Fay, R. R. (1969b) Behavioral audiogram for the goldfish. *J. Aud. Res.* 9, 112-121
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- Offutt, G.C. (1968) Auditory response in the goldfish. *J. Aud. Res.* 8, 391-400.
- Popper, A. N. (1971) The effects of size on auditory capacities of the goldfish. *J. Aud. Res.* 11, 239-247.
- Weiss, B. A. (1966) Auditory sensitivity in the goldfish. *J. Aud. Res.* 6, 321-335.

Table F1-0. Sound pressure audiograms for *Carassius auratus* (goldfish).

Frequency (Hz)	Sound Pressure Threshold (dB re: 1 dyne cm ⁻²)						
	1	2	3	4	5	6	7
30		-22					
40				-4			
50	-6	-24	-24.6				
70		-23					
100	-17	-25.5	-28.4	-18	-23.8	-26.2	33
150							-4
200	-26	-33	-41.7				-15
250							-2
300					-42.5	-46.2	-14
350		-37					
400	-31.5			-22			-17.5
500			-45.6		-44.9	-48.2	-15
600		-31.5					-15
700							-20
800		-25	-44.5	-27			-4
900							-12.5
1000	-39.5	-23	-43.1		-42.8	-39.9	-11.5
1455		-4					
1500	-44		-27.9	5	-24.8	-26.4	-6.5
1776		8					
2000	-40		-1.8		0.7	-5.4	10
2360		16.5					
2500					11.4	10.9	10.8
3000	-32.5		22.3	45			32
4000	-23						
5000	-13.5						
8000				52			

Notes:

1- Loudspeaker in air. Conditioned snapping for food. This experiment also included a comparison with thresholds for an underwater sound projector, showing significantly lower thresholds at frequencies below 500 Hz. These thresholds are not plotted here. In a companion experiment, Enger (1966) manipulated underwater sound source distance (Fig. F18-0 plots these results along with the results of other sound source distance experiments).

2- Loudspeaker in air. Classical conditioning of respiration using descending method of limits. Means: N=4.

3- Loudspeaker in air. Instrumental avoidance conditioning using the staircase psychophysical procedure. Means: N=4.

4- Underwater speaker (J9). Classical heart rate conditioning using the descending method of limits. Means: N=31.

5-6 Loudspeaker in air. Instrumental avoidance conditioning using the staircase psychophysical procedure. No significant statistical differences in threshold were found between 45-48 mm fish (#5) and 110-120 mm fish (#6). Means: N=6 in each group.

7- Underwater speakers (J9) facing each other, operated 180° out of phase. This arrangement likely produced an acoustic field with minimum sound pressure and maximum particle motion. Instrumental avoidance conditioning using the staircase psychophysical procedure. Means: N=3.

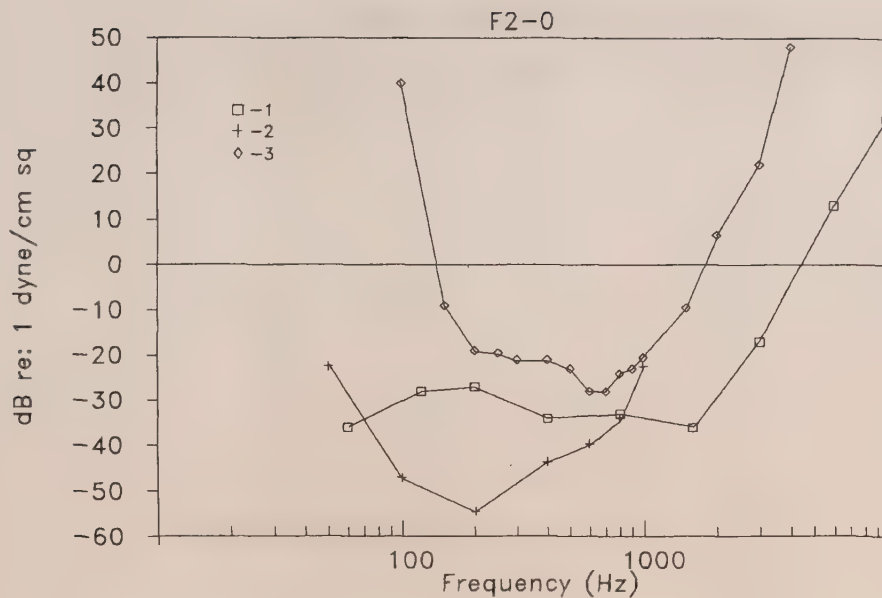


Fig. F2-0. Sound pressure audiograms for catfish.

- 1- *Amiurus nebulosus* - catfish (Poggendorf, 1952)
- 2- *Arius felis* - marine catfish (Popper and Tavalga, 1981)
- 3- *Ictalurus nebulosus* - catfish (Weiss, Strother, and Hartig, 1969)

References:

- Poggendorf, D. (1952) Die absoluten Hörschwellen des Zwergwelses (*Amiurus nebulosus*) und Beiträge zur Physik des Weberschen Apparatus der Ostariophysen. Z. verg. Physiol. 34, 222-257.
- Popper, A. N., Tavalga, W. N. (1981) Structure and function in the ear of the marine catfish, *Arius felis*. J. Comp. Physiol. 144, 27-34.
- Weiss, B. A., Strother, W. F. and Hartig, G. M. (1969) Auditory sensitivity in the bullhead catfish (*Ictalurus nebulosus*). Proc. Nat. Acad. Sci. 64, 552-556.

Table F2-0. Sound pressure audiograms for catfish.

Frequency (Hz)	Sound Pressure Threshold (dB re: 1 dyne cm ⁻²)		
	1	2	3
50		-22.4	
60	-36		
100		-47	40
120	-28		
150			-9
200	-27	-54.5	-19
250			-19.5
300			-21
400	-34	-43.6	-21
500			-23
600		-39.6	-28
700			-28
800	-33	-34	-24
900			-23
1000		-22.5	-20.5
1500			-9.5
1600	-36		
2000			6.5
3000	-17		22
4000			48
6000	13		
10000	32		

Notes:

Amiurus nebulosus and *Ictalurus nebulosus* are different names for the same species, the bullhead catfish. *Ictalurus* is preferred. See Popper and Tavalga (1981) for the structure of the ear of the marine catfish, unusual for the great size of the utricular otolith.

1- Underwater loudspeaker at tank bottom. Conditioned approach for food using the descending method of limits. Thresholds shown are for the animal with the most complete data and with the greatest sensitivity of the 8 animals tested (A4). Thresholds were measured as a function of the animal's vertical position in the tank, and the data shown are for a middle position. Means: N=1.

2- Loudspeaker in air. Instrumental shock avoidance (barrier crossing) using the staircase psychophysical procedure. Means: N=10.

3- Underwater sound projector (J9) operated 180° out of phase, facing each other. This likely produced a sound field having a minimum sound pressure component and a large particle displacement component. Acoustic particle motion was not measured. Instrumental shock avoidance (tank crossing) using the staircase psychophysical procedure.

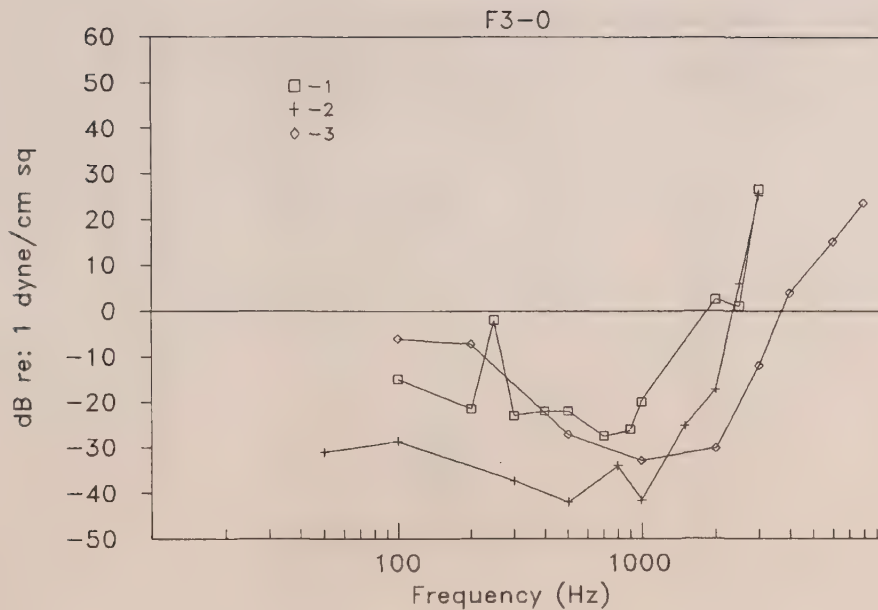


Fig. F3-0. Sound pressure detection thresholds for carp.

- 1- *Cyprinus carpio* - Japanese carp (Kohler, 1973)
- 2- *Cyprinus carpio* - carp (Popper, 1972)
- 3- *Carassius carassius* - goldfish (Siegmund and Wolff, 1973)

References:

- Kohler, D. (1973) A behavioural audiogram of juvenile carp. *Experientia*, 29, 125-127.
- Popper, A. N. (1972). Pure-tone auditory thresholds for the carp, *Cyprinus carpio*. *J. Acoust. Soc. Amer.* 52, 1714-1717.
- Siegmund, R., Wolff, D.K. (1973) Experimentelle Untersuchungen zur Bestimmung des Hörvermögens der Karausche (*Carassius carassius* L.). *Fisch. Forsch.* 11, 117-124.

Table F3-0. Sound pressure detection thresholds for carp.

Frequency (Hz)	Sound Pressure (dB re: 1 dyne cm ⁻²)		
	1	2	3
50		-31	
100	-15	-28.6	-6.1
200	-21.5		-7.2
250	-2		
300	-23	-37.4	
400	-22		
500	-22	-42	-27.2
700	-27.5		
800		-34	
900	-26		
1000	-20	-41.6	-32.9
1500		-25.2	
2000	2.5	-17.2	-30.2
2500	1	5.9	
3000	26.5	25.1	-12
4000			3.8
6000			15
8000			23.5

Notes:

1- Underwater loudspeaker. Instrumental avoidance using an unspecified psychophysical procedure. Means: N=1.

2- Loudspeaker in air. Instrumental avoidance using the staircase psychophysical procedure. Means: N=6.

3- Underwater loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Means: N=5.

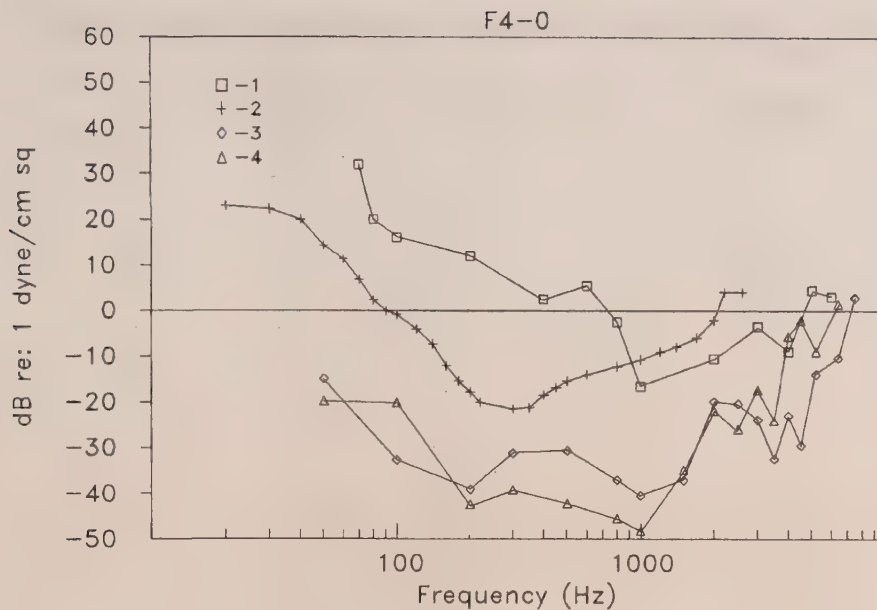


Fig. F4-0. Sound pressure thresholds for several otophysan species (species having Weberian ossicles).

- 1- *Leucaspius delineatus* - a minnow (von Schade, 1971)
- 2- *Semotilus atromaculatus* - a creek chub (Kleerekoper and Chagnon, 1954)
- 3- *Astyanax mexicanus* - Mexican tetra (Popper, 1970)
- 4- *Astyanax jordani* - Mexican blind cave fish (Popper, 1970)

References:

- Kleerekoper, H. and Chagnon, E.C. (1954) Hearing in fish with special reference to *Semotilus atromaculatus atromaculatus* (Mitchill). J. Fish. Res. Bd. Can. 11, 130-152.
- Popper, A. N. (1970) Auditory capacities of the Mexican blind cave fish (*Astyanax jordani*) and its eyed ancestor (*Astyanax mexicanus*). Anim. Behav. 18, 552-562.
- von Schade, R. (1971) Experimentelle Untersuchungen zum Hörvermögen an *Leucaspius delineatus*. Biol. Zentr. 90, 337- 356.

Table F4-0. Sound pressure thresholds for several otophysan species (species having Weberian ossicles).

Frequency (Hz)	Sound Pressure (dB re: 1 dyne cm ⁻²)*			
	1	2*	3	4
20		22.9		
30		22.3		
40		20.0		
50		14.3	-14.9	-19.7
60		11.4		
70	32	6.8		
80	20	2.3		
90		-0.1		
100	16	-0.9	-32.7	-20.1
120		-4.2		
140		-7.3		
160		-12.0		
180		-15.4		
200	12	-17.7	-39.1	-42.3
220		-20.0		
300		-21.4	-31.2	-39.2
350		-21.1		
400	2.5	-18.4		
450		-16.8		
500		-15.4	-30.6	-42.1
600	5.5	-14.0		
800	-2.5	-12.2	-37	-45.5
1000	-16.5	-10.7	-40.5	-48.2
1200		-9.1		
1400		-7.9		
1500			-37.1	-34.8
1700		-6.0		
2000	-10.5	-2.1	-19.8	-21.8
2200		4.1		
2500			-20.3	-25.9
2600		4.1		
3000	-3.5		-23.8	-17.3
3500			-32.4	-24
4000	-9		-22.9	-5.6
4500			-29.4	-2.2
5000	4.5			
5200			-13.9	-9
6000	3			
6400			-10.3	1.5
7500			2.8	

Notes:

1- Underwater loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Means: N=5.

2- Underwater loudspeaker. Conditioned approach for food. *No absolute sound pressure calibration; thresholds in dB with an arbitrary reference.

3- and 4- *Astyanax jordani* is better known as *Anoptichthys jordani*. Loudspeaker in air. Instrumental avoidance using staircase psychophysics. Thresholds are likely not masked. Means: N=3 to 7 for #5 and N=1 to 5 for #6.

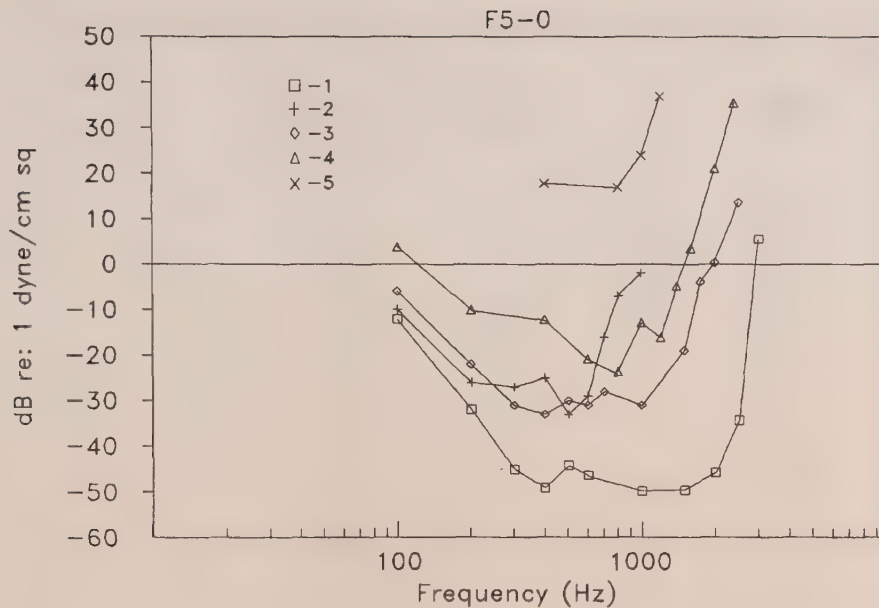


Fig. F5-0. Sound pressure detection thresholds for five non-otophysan "hearing specialists."

- 1- *Myripristus kuntzei* - soldierfish (Coombs and Popper, 1979)
- 2- *Notopterus chitala* - clown knifefish (Coombs and Popper, 1982)
- 3- *Gnathonemus petersii* - elephant nose (McCormick and Popper, 1984)
- 4- *Holocentrus ascensionis* - squirrelfish (Wodinsky and Tavalga, 1964)
- 5- *Sargus annularis* - ringed sea-bream (Dijkgraaf, 1952)

References:

- Coombs, S., and Popper, A.N. (1979) Hearing differences among Hawaiian squirrelfish (family Holocentridae) related to differences in the peripheral auditory system. *J. Comp. Physiol.* 132, 203-207.
- Coombs, S., and Popper, A.N. (1982) Structure and function of the auditory system in the clown knife fish, *Notopterus chitala*. *J. Exp. Biol.* 225-239.
- Dijkgraaf, S. (1952) Über die Schallwahrnehmung bei Meeresfischen. *Z. vergl. Physiol.*, 34, 104-122.
- McCormick, C.A. and Popper, A.N. (1984) Auditory sensitivity and psychophysical tuning curves in the elephant nose fish, *Gnathonemus petersii*. *J. Comp. Physiol.* 155, 753-761.
- Wodinsky, J. and Tavalga, W.N. (1964) Sound detection in teleost fishes. In *Marine Bio-Acoustics*, W.N. Tavalga, (ed), Pergamon Press: Oxford, pp. 269-280.

Table F5-0. Sound pressure detection thresholds for five non-otophysan "hearing specialists."

Frequency (Hz)	Sound Pressure Threshold*				
	(dB re: 1 dyne cm ⁻²)				
	1	2	3	4	5*
100	-12.1	-10	-6	3.8	
200	-31.9	-26	-22	-10	
300	-45	-27	-31		
400	-49.1	-25	-33	-12.2	17.8
500	-44.2	-33	-30		
600	-46.3	-29	-31	-20.9	
700		-16	-28		
800		-7		-23.6	17
1000	-49.8	-2	-31	-12.9	24
1200				-16.1	37
1400				-4.8	
1500	-49.6		-19		
1600				3.5	
1750			-4		
2000	-45.7		0.4	21.1	
2400				35.5	
2500	-34.3		13.7		
3000	5.5				

Notes:

Each of these species has a specialized forward projection of the swimbladder in the region of the ear (sacculle). It is thought that such a connection causes lower sound pressure thresholds and a wider bandwidth of hearing relative to those species without such a connection.

1- This species is of the family Holocentridae, some of which are known to vocalize. Air loudspeaker. Instrumental avoidance using a staircase psychophysical procedure. Thresholds likely not masked by ambient noise. Means: N=2.

2- Air loudspeaker. Instrumental avoidance using a staircase psychophysical procedure. Thresholds likely not masked by ambient noise. Means: N=3.

3- The elephant nose and other mormyrids have recently has been shown to vocalize during courtship. Air loudspeaker. Instrumental avoidance using a staircase psychophysical procedure. Thresholds likely not masked by ambient noise. Means: N=3-4.

4- This squirrelfish of the family Holocentridae is known to produce sounds. Underwater loudspeaker in small water tank. Instrumental avoidance using the staircase psychophysical procedure. Means: N=1-5.

5. Conditioned feeding response. *Sound pressures were measured relatively, and the thresholds are presented in dB with respect to human (graduate student) underwater hearing threshold measured in a large aquarium by the authors.

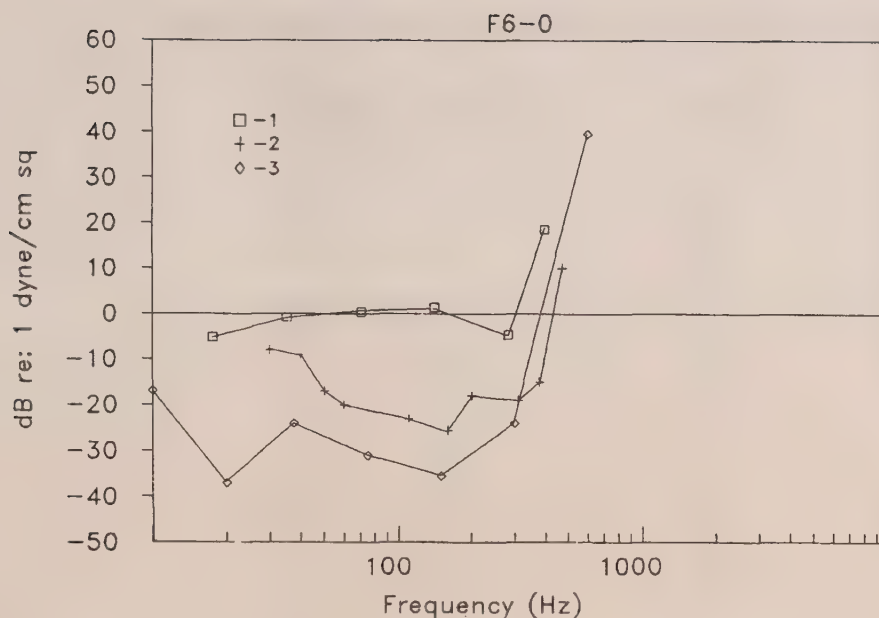


Fig. F6-0. Sound pressure audiograms for *Gadus morhua* (cod).

- 1- Buerkle, 1967
- 2- Chapman and Hawkins, 1973
- 3- Offutt, 1974

References:

- Buerkle, U. (1967) An audiogram of the Atlantic cod, *Gadus morhua* L. J. Fish. Res. Bd. Canada 24, 2309-2319.
- Chapman, C. J. and Hawkins, A.D. (1973) A field study of hearing in the cod, *Gadus morhua* L. J. Comp. Physiol. 85, 147-167.
- Offutt, G. C. (1973) Structures for the detection of acoustic stimuli in the Atlantic codfish, *Gadus morhua*. J. Acoust. Soc. Am. 56, 665-671.

Table F6-0. Sound pressure audiograms for *Gadus morhua* (codfish).

Frequency (Hz)	Sound Pressure Threshold (dB re: 1 dyne cm ⁻²)		
	1	2	3
10			-17
17.6	-5.2		
20			-37
30		-8	
35.3	-0.8		
37.5			-24
40		-9	
50		-17	
60		-20	
70.7	0.4		
75			-31
110		-23	
141	1.3		
150			-35.5
160		-25.5	
200		-18	
283	-4.6		
300			-24
310		-19	
380		-15	
400	18.5		
470		10	
600			39.5

Notes:

1- Underwater loudspeaker (J9) in large concrete tank. Classical cardiac conditioning using descending method of limits. Thresholds below 283 Hz likely masked by ambient noise. Means: N=10.

2- Underwater sound projector (J9) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical method. Thresholds below 200 Hz likely masked by ambient noise. Means: N=43.

3-Loudspeaker in air. Classical cardiac conditioning using the staircase psychophysical procedure. Ambient noise level not specified. Means: N=20.

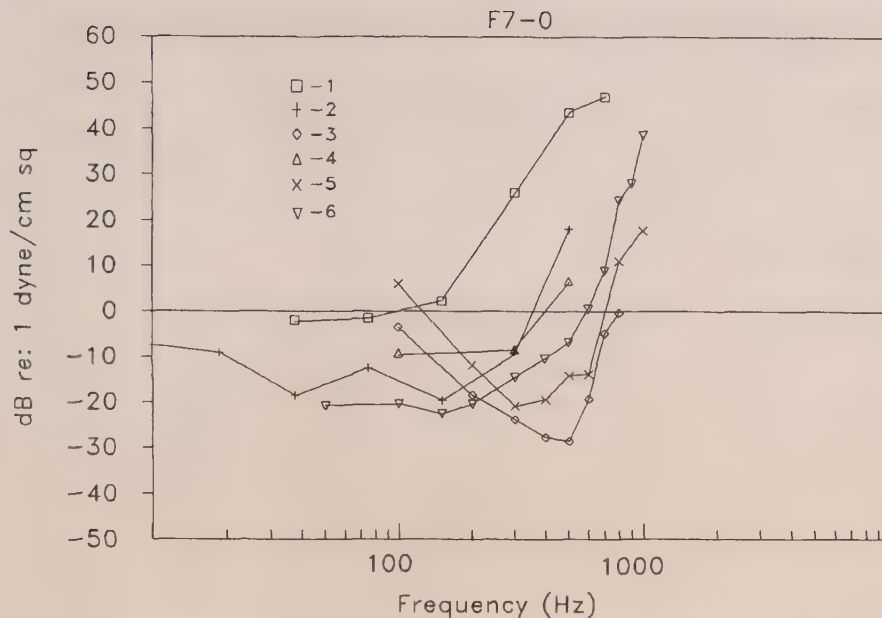


Fig. F7-0. Sound pressure detection thresholds for six fish species without known special adaptations for hearing.

- 1- *Opsanus tau* - toadfish (Fish and Offutt, 1971)
- 2- *Tautoga onitis* - tautog (Offutt, 1971)
- 3- *Adioryx xantherythrus* - Hawaiian squirrelfish (Coombs and Popper, 1979)
- 4- *Tilapia macrocephala* - African mouth-breeder (Tavolga, 1974)
- 5- *Lagodon rhomboides* - pinfish (Tavolga, 1974)
- 6- *Haemulon sciurus* - blue-striped grunt (Tavolga and Wodinsky, 1965)

References:

- Coombs, S., Popper, A.N. (1979) Hearing differences among Hawaiian squirrelfish (family Holocentridae) related to differences in the peripheral auditory system. *J. Comp. Physiol.* 132, 203-207.
- Fish, J.F. and Offutt, G.C. (1972) Hearing thresholds from toadfish, *Opsanus tau*, measured in the laboratory and field. *J. Acoust. Soc. Amer.* 51, 1318-1321.
- Offutt, G.C. (1971) Response of the tautog (*Tautoga onitis*, Teleost) to acoustic stimuli measured by classically conditioning the heart rate. *Conditional Reflex* 6, 205-214.
- Tavolga, W.N. (1974) Signal/noise ratio and the critical band in fishes. *J. Acoust. Soc. Amer.* 55, 1323-1333.
- Tavolga, W.N. and Wodinsky, J. (1965) Auditory capacities in fishes: Threshold variability in the blue-striped grunt, *Haemulon sciurus*. *Anim. Behav.* 13, 301-311.

Table F7-0. Sound pressure detection thresholds for six fish species without known special adaptations for hearing.

Frequency (Hz)	Sound Pressure Threshold (dB re: 1 dyne cm ⁻²)					
	1	2	3	4	5	6
10		-7.5				
18.7		-9				
37.5	-2	-18.5				
50						-20.8
75	-1.5	-12.5				
100			-3.5	-9.2	5.9	-20.4
150	2.2	-19.5				-22.5
200			-18.4		-11.9	-20.4
300	26	-9	-23.8	-8.4	-20.9	-14.5
400			-27.7		-19.4	-10.4
500	43.5	18	-28.5	6.6	-14.1	-6.8
600			-19.3		-13.8	0.5
700	47		-4.8			8.8
800			-0.3		11	24.3
900						28
1000					17.7	38.5

Notes:

1- The toadfish is well known as a sound producer (Fine, 1981). Loudspeaker in air. Classical conditioning of heart rate using the staircase psychophysical procedure. Median of 3 animals. Hearing also tested in the field using a J9 projector at 1.5 meters and an unconditioned, sound-induced suppression of vocalization as the response. Field threshold ranges within 3 dB of the laboratory thresholds at 200 and 400 Hz.

2- Loudspeaker in air. Classical conditioning of heart rate using the staircase psychophysical procedure. N=1 (animal G). Threshold found to be dependent on temperature, with results plotted for 16-19°C. Particle velocity also measured, and thresholds were plotted in terms of particle velocity in the reference.

3- Air loudspeaker. Instrumental avoidance using a staircase psychophysical procedure. Thresholds likely not masked by ambient noise. Means: N=3.

4- Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Means: N=6.

5- Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Means: N=10.

6- Underwater loudspeaker in a small tank. Instrumental avoidance using the staircase psychophysical procedure. Significant individual differences were found particularly at frequencies below 300 Hz. Means: N=6-20.

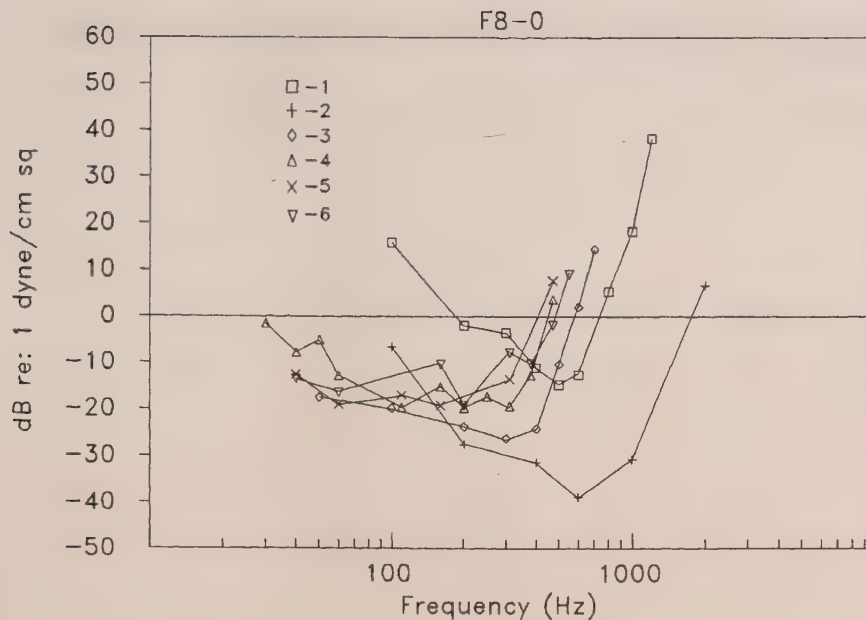


Fig. F8-0. Sound pressure thresholds for six marine species having no known specializations for hearing.

- 1- *Eupomacentrus partitus* - bicolor damselfish (Ha, 1973 as cited in Myrberg and Spire, 1980)
- 2- *Equetus acuminatus* - chubby (Tavolga and Wodinsky, 1963)
- 3- *Albula vulpes* - bonefish (Tavolga, 1974b)
- 4- *Melanogrammus aeglefinus* - haddock (Chapman, 1973)
- 5- *Pollachius pollachius* - pollack (Chapman, 1973)
- 6- *Molva molva* - ling (Chapman, 1973)

References:

- Chapman, C.J. (1973) Field studies of hearing in teleost fish. *Helgoländer wissenschaftliche Meeresuntersuchungen* 24, 371- 390.
- Ha, S. (1973) Aspects of sound communication in the damselfish, *Eupomacentrus partitus*. Doctoral dissertation, University of Miami, FL.
- Myrberg, A.A. Jr., & Spire, J.Y. (1980) Hearing in damselfishes: An analysis of signal detection among closely related species. *J. Comp. Physiol.* 140, 135-144.
- Tavolga, W.N. (1974b) Sensory parameters in communication among coral reef fishes. *Mt. Sinai J. Med.* 41, 324-340.
- Tavolga, W.N. and Wodinsky, J. (1963) Auditory capacities in fishes. Pure tone thresholds in nine species of marine teleosts. *Bull. Amer. Mus. Nat. Hist.* 126, 177-240.

Table F8-0. Sound pressure thresholds for six marine species having no known specializations for hearing.

Frequency (Hz)	Sound Pressure Thresholds (dB re: 1 dyne cm ⁻²)					
	1	2	3	4	5	6
30				-1.6		
40				-7.8	-12.6	-13.6
50			-17.5	-5.1		
60				-12.9	-19	-16.5
100	15.8	-6.6	-19.9			
110				-19.6	-17	
160				-15.1	-19.2	-10.4
200	-2	-27.5	-23.7	-19.7		-19.2
250				-17.3		
300	-3.5		-26.1			
310				-19.3	-13.5	-7.8
380				-12.7		-10.2
400	-11.1	-31.3	-24.1			
470				3.7	7.7	-2
500	-14.7		-10.3			
550						9
600	-12.6	-38.8	2			
700			14.5			
800	5.4					
1000	18.2	-30.7				
1200	38.2					
2000		6.7				
N=	2	3	1	9	2	1

Notes:

1- Underwater sound projector (J9) in one end of a 15 cm diam glass tube with sound absorbers at the opposite end. The response measure was a classically conditioned downward swimming using shock as the unconditioned stimulus. The staircase psychophysical procedure was used. Both sound pressure and particle motion were measured. Noise levels were measured. Confidence intervals were computed for each threshold. It was determined that at 100 Hz, the response to sound was mediated by direct detection of particle motion, but that pressure was the relevant variable above 100 Hz.

2- Underwater loudspeaker in a small water tank. Instrumental avoidance using the staircase psychophysical procedure.

3- Underwater loudspeaker in a small water tank. Instrumental avoidance using the staircase psychophysical procedure. Thresholds below 400 Hz likely masked by ambient noise.

4-6 Underwater loudspeaker (J9) in a free acoustic field. Classical cardiac conditioning using the staircase psychophysical procedure. Thresholds at and below 380 Hz likely masked by ambient noise.

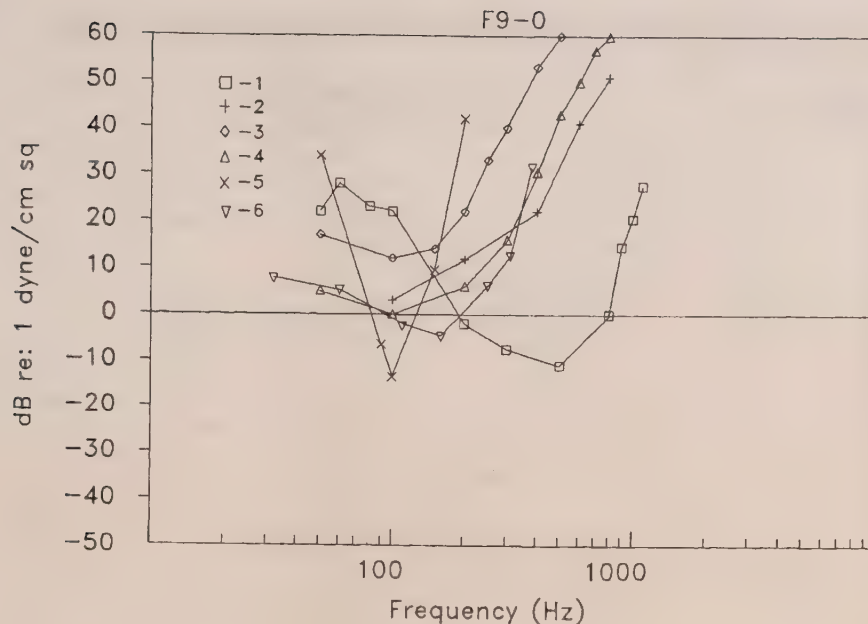


Fig. F9-0. Sound pressure detection thresholds for six fish species having no known hearing specializations.

- 1- *Thunnus albacares* - yellowfin tuna (Iversen, 1967)
- 2- *Gobius niger* - a goby (Dijkgraaf, 1952)
- 3- *Acerina cernua* - ruff (Wolff, 1968)
- 4- *Lucioperca sandra* - pike perch (Wolff, 1968)
- 5- *Perca fluviatilis* - a perch (Wolff, 1967)
- 6- *Salmo salar* - Atlantic salmon (Hawkins and Johnstone, 1978)

References:

- Dijkgraaf, S. (1952) Über die Schallwahrnehmung bei Meeresfischen. *Z. vergl. Physiol.* 34, 104-122.
- Hawkins, A.D., Johnstone, A.D.F. (1978) The hearing of the Atlantic salmon, *Salmo salar*. *J. Fish. Biol.* 13, 655-673.
- Iversen, R. (1967) Response of the yellowfin tuna (*Thunnus albacares*) to underwater sound. In W.N. Tavolga (ed), *Marine Bio-Acoustics*, Vol 2. Pergamon Press: Oxford, pp. 105-121.
- Wolff, D.L. (1967) Das Hörvermögen des Flussbarsches (*Perca fluviatilis* L.) *Biol. Zentr.* 86, 449-460.
- Wolff, D.L. (1968) Das Hörvermögen des Kaulbarsches (*Acerina cernua* L.) und des Zanders, (*Lucioperca sandra* Cuv. und Val.). *Z. vergl. Physiol.* 60, 14-33.

Table F9-0. Sound pressure detection thresholds for six fish species having no known hearing specializations.

Frequency (Hz)	Sound Pressure Threshold*					
	1	2*	3	4	5	6
32						7.5
50	22		17	5	34	
60	28					5
80	23					
90					-6.5	
100	22	3	12	0	-13.5	
110						-2.5
150			14		9.5	
160						-4.8
200	-2	11.8	22	6	42	
250			33			6
300	-7.5		40	16		
310						12.5
380						31.5
400		22	53.2	30.5		
500	-11		60	43		
600		41		50		
700				57		
800	0	51		60		
900	14.5					
1000	20.5					
1100	27.5					

Notes:

1- Underwater sound projector (J9) in a large pen. Conditioned turning while swimming (two alternative forced choice) for food using descending method of limits. Median: N=2.

2- Conditioned feeding response. *Sound pressures were measured relatively, and the thresholds are presented in dB with respect to human underwater hearing threshold.

3- Underwater loudspeaker in a small water tank. Instrumental avoidance using staircase psychophysics. Means: N=5.

4- Underwater loudspeaker in a small water tank. Instrumental avoidance using staircase psychophysics. Means: N=4.

5- Underwater loudspeaker in a large water tank. Classical conditioning of fish movement using the staircase psychophysical procedure. N=1.

6- Underwater sound projectors (J9 and J11) in a free acoustic field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=5. Thresholds varied as a function of source distance (.65-2.7 m) below 200 Hz. Thresholds plotted are medians across all source distances. Sound pressure and particle motion were measured, and sound detection was found to be based on the direct detection of particle motion. Best sensitivity at 160 Hz of -86 dB re: 1 micron (see Fig. F15-0).

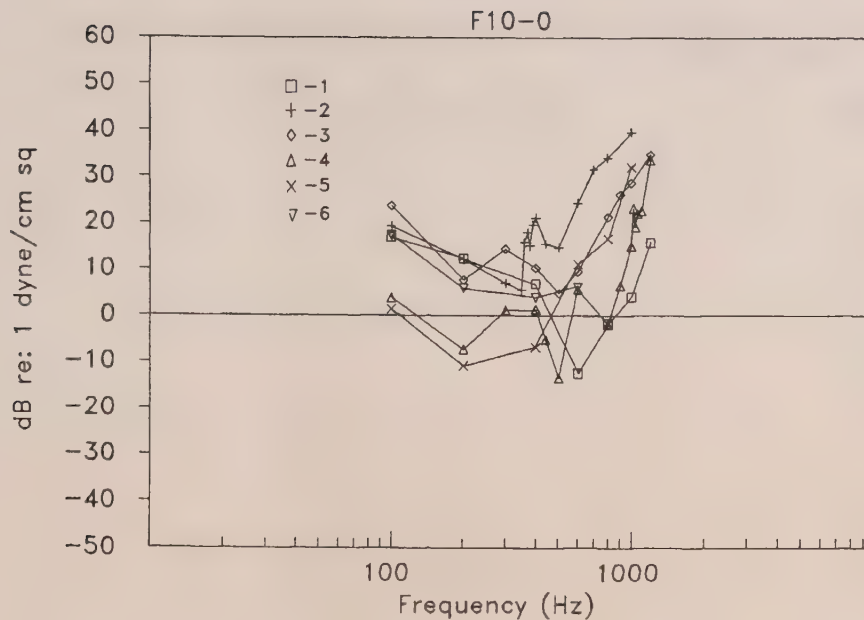


Fig. F10-0. Sound pressure detection thresholds for six marine species having no known auditory specializations (Tavolga and Wodinsky, 1963).

- 1- *Holocentrus vexillarius* - dusky squirrelfish
- 2- *Lutjanus apodus* - schoolmaster
- 3- *Thalassoma bifasciatum* - blue-head wrasse
- 4- *Eupomacentrus leucostictus* - beau-gregory
- 5- *Epinephelus guttatus* - red hind
- 6- *Prionotus scitulus* - slender sea robin

Reference:

Tavolga, W.N. and Wodinsky, J. (1963) Auditory capacities in fishes. Pure tone thresholds in nine species of marine teleosts. Bull. Amer. Mus. Nat. Hist. 126, 177-240.

Table F10-0. Sound pressure detection thresholds for six marine species having no known auditory specializations.

Frequency (Hz)	Sound Pressure Thresholds (dB re: 1 dyne cm ⁻²)					
	1	2	3	4	5	6
100	16.9	19.3	23.7	3.8	1.4	17.4
200	12.4	12.1	7.7	-7.3	-10.9	5.9
300		7	14.4	1.1		
350		5.5				
360		15.8				
370		18				
380		15.1				
390		19.6				
400	6.9	21.2	10.3	1.3	-6.8	3.9
440		15.5		-5.2		
500		14.7	4.8	-13.4		
600	-12.4	24.3	9.5	5.6	11.1	6.2
700		31.6				
800	-1.6	34.1	21.4	-2	16.6	
900			26.1	6.5		
1000	4	39.6	28.7	15	32.1	
1020				23.2		
1040				19.2		
1060				22.1		
1100				22.7		
1200	15.8		34.8	33.7		
N=	3	2	4	6	1	1

Notes:

This a classic study of the hearing of several marine species carefully studied using the same set of procedures. Three additional species were studied and are plotted elsewhere; *E. acuminatus* in Fig. F8-0, and *H. ascensionis* in Fig. F5-0 (based on more detailed work on this species by Wodinsky and Tavalga, 1964), and *H. sciurus* in Fig. F7-0 (based on more detailed work on this species by Tavalga and Wodinsky, 1965).

In several cases, two sets of low frequency thresholds were obtained; one set of high thresholds early in training and another set of lower thresholds later in training. These were observed in *L. apodus*, *T. bifasciatum*, *E. leucostictus*, and *H. sciurus* (thresholds for this species plotted in Fig. F7-0 from a later and more complete study by Tavalga and Wodinsky, 1965). The authors interpreted the latter lower thresholds as possibly due to detection of near field particle motion by the lateral line system. This lateral line hypothesis is presently doubtful since the otolith organs of the ear are likely more sensitive to particle motion than the lateral line organs. For those species showing two sets of thresholds, the median of the lower (later) thresholds was computed and plotted here.

Underwater loudspeaker in a small water tank. Instrumental avoidance using the staircase psychophysical procedure.

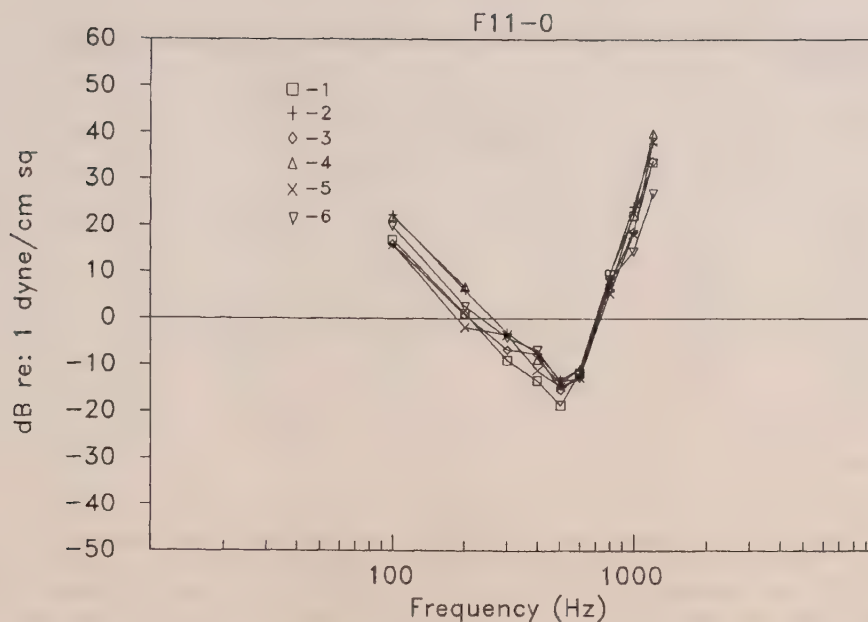


Fig. F11-0. Sound pressure detection thresholds for six damselfishes of the genus *Eupomacentrus* (Myrberg and Spires, 1980).

- 1- *E. dorsopunicans* - (a damselfish)
- 2- *E. planiformes* - threespot damselfish
- 3- *E. diencaeus* - longfin damselfish
- 4- *E. leucostictus* - beau-gregory
- 5- *E. variabilis* - cocoa damselfish
- 6- *E. mellis* - honey gregory (likely a juvenile of *E. diencaeus*)

References:

- Myrberg, A.A. Jr., & Spires, J.Y. (1980) Hearing in damselfishes: an analysis of signal detection among closely related species. *J. Comp. Physiol.* 140, 135-144.

Table F11-0. Sound pressure detection thresholds for six damselfishes of the genus *Eupomacentrus*.

Frequency (Hz)	Sound Pressure Threshold (dB re: 1 dyne cm ⁻²)					
	1	2	3	4	5	6
100	16.9	22.3	16	22	15.8	19.8
200	1	6	0.7	6.7	-2	2.5
300	-9	-3.1	-6.7		-3.5	-4.2
400	-13.3	-7.5	-7.7	-8.7	-11.1	-6.8
500	-18.6	-13.2	-15.3	-14	-14.7	-13.6
600	-11.7	-10.8	-12.5	-10.8	-12.6	-12.7
800	9.5	9.3	7.3	6.7	5.4	8.2
1000	22.2	24.2	18.7	22.3	18.2	14.4
1200	33.8	37.8	34	40	38.2	27
N=	4	4	2	4	3	2

Notes:

This is a most complete and elegant study of the hearing of closely related species. See Fig. F8-0 for data on a seventh damselfish, *E. partitus* (Ha, 1973 as cited by Myrberg and Spires, 1980). Damselfishes (family Pomacentridae) are sound producers and use sound in territorial and other social behavior (Myrberg, Spanier, and Ha, 1978). However, they are not known to have specialized structures for the detection of sound.

Underwater sound projector (J9) in one end of a 15 cm diam glass tube with sound absorbers at the opposite end. The response measure was a classically conditioned downward swimming using shock as the unconditioned stimulus. The staircase psychophysical procedure was used. Both sound pressure and particle motion were measured. Noise levels were measured. Confidence intervals were computed for each threshold. It was determined that at 100 Hz, the response to sound was mediated by direct detection of particle motion, but that pressure was the relevant variable above 100 Hz.

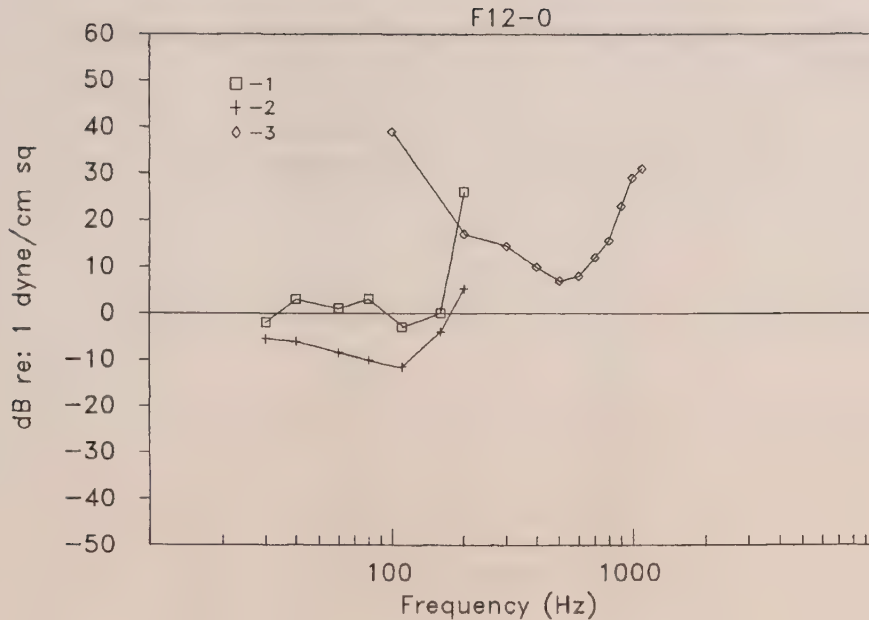


Fig. F12-0. Sound pressure sensitivity for three teleost species lacking a swimbladder.

- 1- *Pleuronectes platessa* - plaice (Chapman and Sand, 1974)
- 2- *Limanda limanda* - dab (Chapman and Sand, 1974)
- 3- *Euthynnus affinis* - tuna (kawakawa) (Iversen, 1969)

References:

- Chapman, C.J. and Sand, O. (1974) Field studies of hearing in two species of flatfish, *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). *Comp. Biochem. Physiol.* 47A, 371-385.
- Iversen, R.T.B. (1969) Auditory thresholds of the scombrid fish *Euthynnus affinis*, with comments on the use of sound in tuna fishing. *FAO Conference on Fish Behavior in Relation to Fishing Techniques and Tactics*. *FAO Fisheries Rep.* No. 62. 3, 849-859.

Table F12-0. Sound pressure sensitivity for three teleost species lacking a swimbladder.

Frequency (Hz)	Sound Pressure (dB re: 1 dyne cm ⁻²)		
	1	2	3
30	-2	-5.5	
40	3	-6.2	
60	1	-8.5	
80	3	-10.2	
100			39
110	-3	-11.5	
160	0	-4	
200	26	5.3	17
300			14.5
400			10
500			7
600			8
700			12
800			15.5
900			23
1000			29
1100			31

Notes:

1- and 2- The authors determined that these species detected acoustic particle motion directly, and that thresholds expressed in terms of sound pressure have little meaning. The sound pressure thresholds are given here to facilitate comparisons with the sound pressure thresholds of other species for which the relevant acoustic intensity parameter (i.e. pressure or displacement) was not determined. Sound pressure thresholds were determined for sound source distances of 3 meters and 0.7 meters (see also Fig. F18-0). The thresholds at the 3 meter distance, plotted here, are about 6-12 dB higher than those at the shorter distance. It is likely that some of these thresholds were masked by ambient noise.

Underwater sound projector (J9) in a free acoustic field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=1 for plaice (*P. platessa*), N=2 for dabs (*L. limanda*).

3- It is likely that this species responds directly to acoustic particle motion as well, although the author did not test this. It is also likely that some of these thresholds were masked by ambient noise which is likely greater at low frequencies. Two alternative forced choice for a food reward using a descending method of limits. Means: N=2.

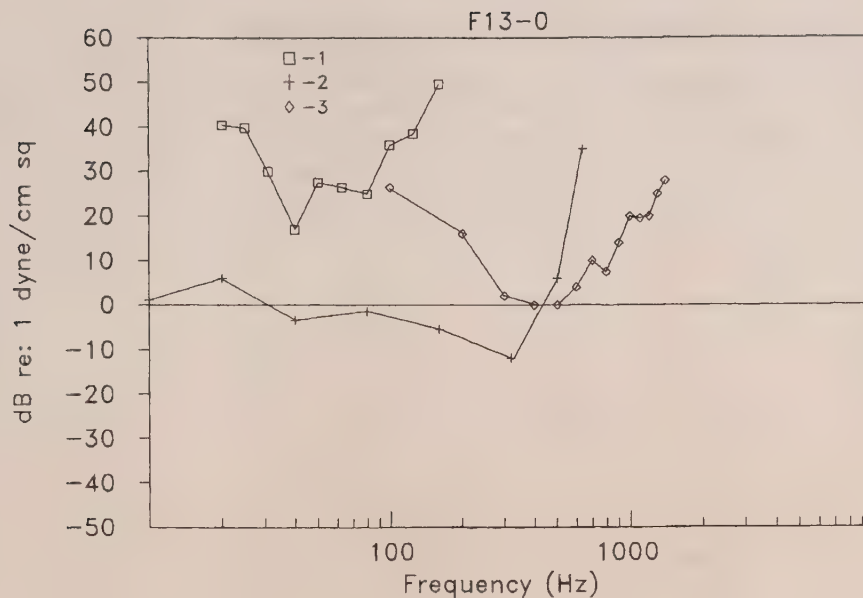


Fig. F13-0. Sound pressure thresholds for three shark species.

- 1- *Heterodontus francisci* - horn shark (Kelly and Nelson, 1975)
- 2- *Negaprion brevirostris* - lemon shark (Banner, 1967)
- 3- *Carcharhinus leucas* - bull shark (Kritzler and Wood, 1961)

References:

- Banner, A. (1967) Evidence of sensitivity to acoustic displacements in the lemon shark, *Negaprion brevirostris* (Poey). In P.H. Cahn (ed), Lateral Line Detectors. Indiana University Press: Bloomington, pp. 265-273.
- Kelly, J.C., Nelson, D.R. (1975) Hearing thresholds of the horn shark, *Heterodontus francisci*. J. Acoust. Soc. Amer. 58, 905-909.
- Kritzler, H., Wood, L. (1961) Provisional audiogram for the shark, *Carcharhinus leucas*. Science 133, 1480-1482.

Table F13-0. Sound pressure thresholds for three shark species.

Frequency (Hz)	Sound Pressure* (dB re: 1 dyne cm ⁻²)		
	1	2	3*
10		1	
20	40.5	6	
25	39.8		
31	30		
40	17	-3.5	
50	27.5		
63	26.5		
80	25	-1.5	
100	36		26.5
125	38.5		
160	49.5	-5.5	
200			16
300			2
320		-12	
400			0
500		6	0
600			4
640		35	
700			10
800			7.5
900			14
1000			20
1100			19.5
1200			20
1300			25
1400			28

Notes:

(See also notes for Fig. F14-0.)

1- Underwater sound projector (J9) in a large wood tank. Classical cardiac conditioning using the staircase psychophysical procedure. Both sound pressure and acoustic particle displacement were measured. Pressure thresholds varied as a function of source distance (0.3 and 0.6 m), while particle motion thresholds did not. Thresholds plotted are for 0.3 meter source distance. It is likely that these thresholds were masked by ambient noise at 80 Hz and below. Means: N=4.

2- Underwater sound projector (J9) at one end of a 15 cm diam glass tube containing the shark. Classical respiratory conditioning using a staircase psychophysical procedure. Both sound pressure and acoustic particle displacement were measured. Thresholds likely masked by ambient noise. Means: N=19.

3- Underwater loudspeaker in a sea pen. Conditioned turning and approach to the sound source using the descending method of limits. Acoustic particle motion not measured. *The thresholds for *C. leucas* are expressed in dB with reference to an unspecified acoustic noise level. Means: N=1.

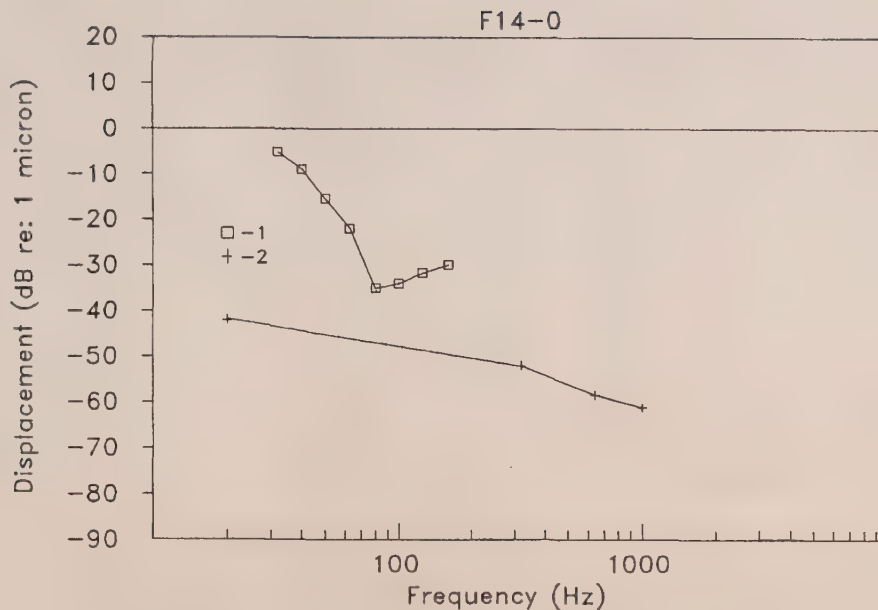


Fig. F14-0. Acoustic particle displacement detection thresholds for two shark species.

- 1- *Heterodontus francisci* - horn shark (Kelly and Nelson, 1975)
- 2- *Negaprion brevirostris* - lemon shark (Banner, 1967)

References:

- Banner, A. (1967) Evidence of sensitivity to acoustic displacements in the lemon shark, *Negaprion brevirostris* (Poey). In P.H. Cahn, (ed), Lateral Line Detectors. Indiana University Press: Bloomington, pp. 265-273.
- Kelly, J.C., Nelson, D.R. (1975) Hearing thresholds of the horn shark, *Heterodontus francisci*. J. Acoust. Soc. Amer. 58, 905-909.

Table F14-0. Acoustic particle displacement detection thresholds for two shark species.

Frequency (Hz)	Particle Displacement (dB re: 1 micron)	
	1	2
20		-42
32	-5.2	
40	-9	
50	-15.4	
63	-22	
80	-35	
100	-34	
125	-31.7	
160	-29.9	
320		-52
640		-58.4
1000		-61.1

Notes:

1- Underwater sound projector (J9) in a large wood tank. Classical cardiac conditioning using the staircase psychophysical procedure. Both sound pressure and acoustic particle displacement were measured in this experiment. Thresholds were determined at two source distances (0.3 and 0.6 meters). Thresholds did not vary systematically with distance. The thresholds plotted are averaged across the two distance conditions. It is likely that these thresholds were masked by ambient noise at frequencies of 80 Hz and below. Means: N=4.

2- Underwater sound projector (J9) at one end of a 15 cm diam glass tube containing the shark. Classical respiratory conditioning using staircase psychophysics. Both sound pressure and acoustic particle displacement were measured in this experiment. Thresholds likely masked by ambient noise. Means: N=19.

Banner (1967) showed that the lemon shark, *N. brevirostris*, detects acoustic particle motion directly, and is not sensitive to sound pressure. This is consistent with the shark lacking a swimbladder. It is likely that all sharks are similarly sensitive to particle motion rather than to sound pressure at detection threshold. Note, however, that van den Berg and Schuijf (1983) found that the shark *Chiloscyllium griseum* could discriminate between sounds based on the phase difference between particle motion and acoustic pressure, thus showing that sound pressure information is processed above detection threshold.

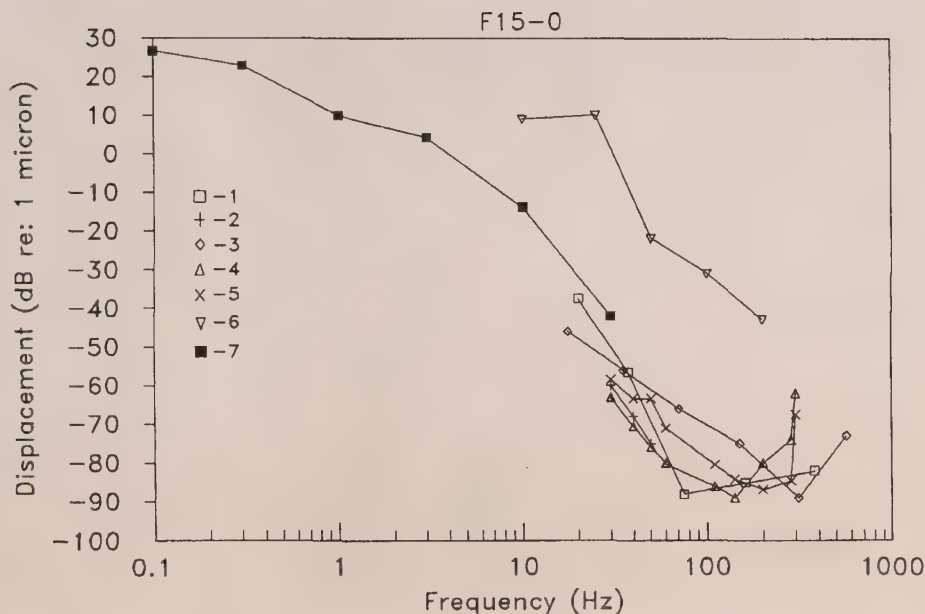


Fig. F15-0. Particle displacement detection thresholds for several fish species.

- 1- *Gadus morhua* - cod (Offutt, 1974)
- 2- *Gadus morhua* - cod (Chapman and Hawkins, 1973)
- 3- *Gadus morhua* - cod (Buerkle, 1967)
- 4- *Pleuronectes platessa* - plaice (Chapman and Sand, 1974)
- 5- *Limanda limanda* - dab (Chapman and Sand, 1974)
- 6- *Carassius auratus* - goldfish (Fay and Patricoski, 1980)
- 7- *Gadus morhua* - cod (Sand and Karlsen, 1986)

References:

- Buerkle, U. (1967) An audiogram of the Atlantic cod, *Gadus morhua* L. J. Fish. Res. Bd. Canada. 24, 2309-2319.
- Chapman, C. J. and Hawkins, A.D. (1973) A field study of hearing in the cod, *Gadus morhua* L. J. Comp. Physiol. 85, 147-167.
- Chapman, C. J. and Sand, O. (1974) Field studies of hearing in two species of flatfish, *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). Comp. Biochem. Physiol. 47A, 371-385.
- Fay, R.R., Patricoski, M.L. (1980) Sensory mechanisms of low frequency vibration detection in fishes. In R. Buskirk (ed), Abnormal Animal Behavior Proceeding Earthquakes. Conference II. U.S. Geological Survey Open File Report, 80-453.
- Offutt, G. C. (1973) Structures for the detection of acoustic stimuli in the Atlantic Codfish, *Gadus morhua*. J. Acoust. Soc. Am. 56, 665-671.
- Sand, O. and Karlsen, H.E. (1986) Detection of infrasound by the atlantic cod. J. Exp. Biol. 125, 197-204.

Table F15-0. Particle displacement detection thresholds for several fish species.

Frequency (Hz)	Particle Displacement (dB re: 1 micron)						
	1	2	3	4	5	6	7
0.1							26.7
0.3							11.9
1							10
3							4.4
10						9	-13.9
17.6			-46				
20	-37.5						
25						10	
30		-60		-63	-58		-42.1
35.3			-56				
37.5	-56.5						
40		-68		-70.5	-63.3		
50		-75		-75.9	-63.3	-22	
60				-80	-71		
70.7			-66				
75	-88						
80				-86	-80.4		
100						-31	
110				-88.9	-84		
141			-75				
150	-85						
160				-80	-86.7		
200				-74	-84.6	-43	
250				-61.9	-67.5		
283			-89				
300	-82						
400			-73				

Notes:

1- Loudspeaker in air. Classical cardiac conditioning using the staircase procedure. Velocity measured and displacement at threshold calculated. Means: N=20.

2- Underwater sound projector (J9) in a free field. Classical cardiac conditioning using the staircase method. Thresholds below 200 Hz likely masked by ambient noise. Sound pressure threshold varied as a function of source distance at frequencies below 50 Hz, suggesting sensitivity to particle motion. Displacements based on calculations from sound pressure measurements within the near field. Means: N=43.

3- Underwater loudspeaker (J9) in large concrete tank. Classical cardiac conditioning using descending method of limits. Thresholds below 283 Hz likely masked by ambient noise. Displacement calculated from sound pressure measurements.

4-5- Underwater loudspeaker (J9) in free field. Classical cardiac conditioning using staircase method. Thresholds varied with source distance indicating displacement sensitivity. Thresholds calculated from near field pressures. Means: N=3 and 4.

6- Direct vertical vibration of animal's head. Classical respiratory conditioning using staircase psychophysics. Head motion measurement with accelerometer. Means: N=4.

7- Classical cardiac conditioning using the staircase procedure. Animal in a closed tube with sound projectors at each end operating 180° out of phase (push-pull). This produced a uniform displacement field. Rise/fall times from 2 to 5 cycles of the wave. Data are means of at least 6 animals. Thresholds were reported in terms of acceleration, and were converted to RMS displacement (in microns) for this figure.

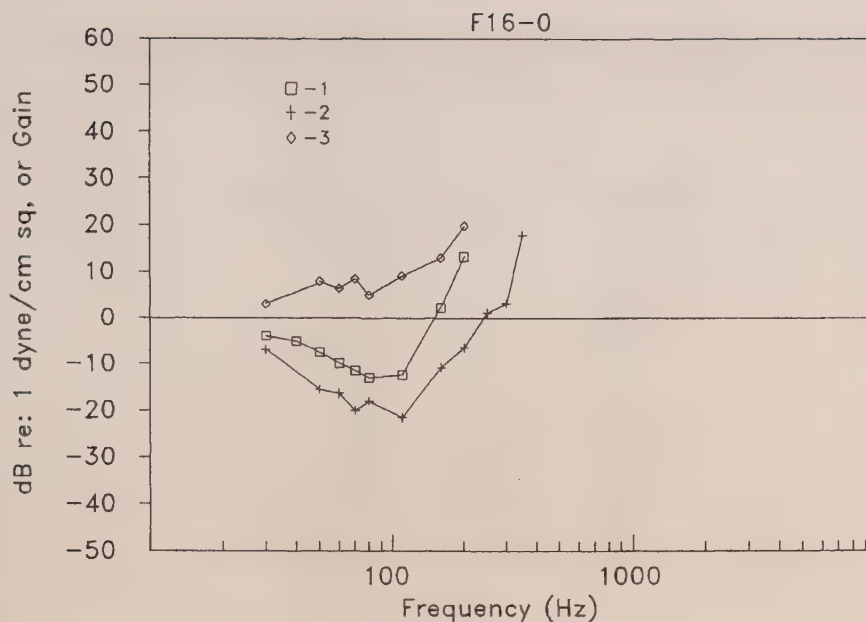


Fig. F16-0. Sound pressure thresholds for *Limanda limanda* (dab) with and without a small air-filled balloon beneath the head of the fish, and the difference between these two thresholds (Chapman and Sand, 1974).

- 1- Normal
- 2- With bubble
- 3- Gain due to bubble

References:

Chapman, C.J. and Sand, O. (1974) Field studies of hearing in two species of flatfish, *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). Comp. Biochem. Physiol. 47, 371-385.

Table F16-0. Sound pressure thresholds for the dab (*Limanda limanda*) with and without a small air-filled balloon beneath the head of the fish, and the difference between these two thresholds (Chapman and Sand, 1974).

Frequency (Hz)	Sound Pressure or Gain (dB re: 1 dyne cm ⁻²)		
	1	2	3
30	-4	-7	3
40	-5.2		
50	-7.5	-15.5	8
60	-9.8	-16.3	6.4
70	-11.5	-20	8.5
80	-13	-18	5
110	-12.4	-21.5	9.1
160	2.3	-10.8	13
200	13.3	-6.5	19.8
250		1.1	
300		3.3	
350		17.8	

Notes:

Underwater sound projector (J9) in a free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=2.

This species lacks a swimbladder and was shown to be sensitive to acoustic particle displacement, and not to sound pressure. The experiment illustrated here was performed to demonstrate the possible function of a swimbladder for hearing in fishes. The results show that a gas bubble near the head lowers sound pressure thresholds and widens the bandwidth of hearing relative to the case without it. Column #3 shows the gain in sound pressure sensitivity caused by the bubble.

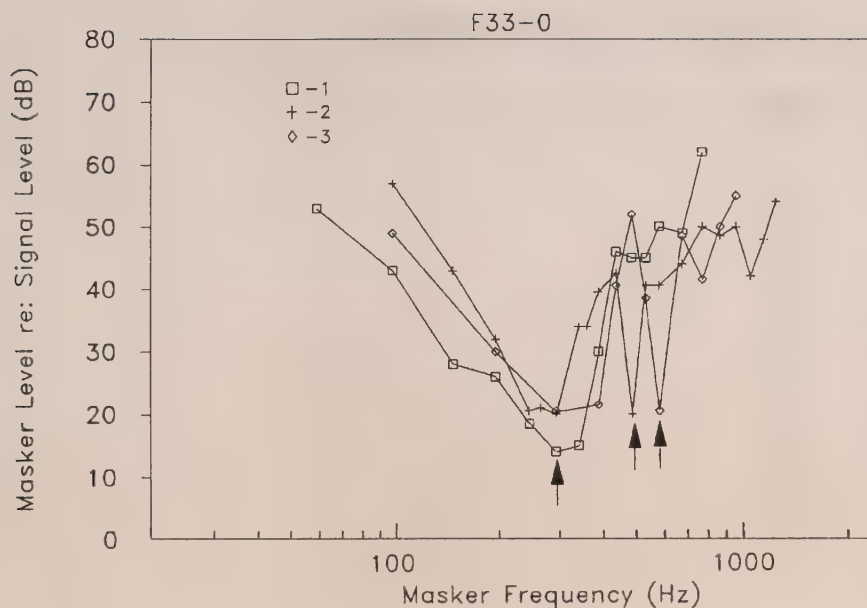


Fig. F17-0. The effect of swimbladder mutilation and malleus extirpation on hearing sensitivity in *Ictalurus nebulosus* (bullhead catfish).

- 1- Swimbladder mutilation (Kleerekoper and Roggenkamp (1959)
- 2- Malleus extirpation (Poggendorf, 1952)

References:

- Kleerekoper, H. and Roggenkamp, P.A. (1959) An experimental study on the effect of the swimbladder on hearing sensitivity in *Ameiurus nebulosus nebulosus* (LeSueur). Can. J. Zool. 37, 1-8.
- Poggendorf, D. (1952) Die absoluten Hörschwellen des Zwergwelses (*Amiurus nebulosus*) und Beiträge zur Physik des Weberschen Apparatus der Ostariophysen. Z. vergl. Physiol. 34, 222-257.

Table F17-0. The effect of swimbladder mutilation and malleus extirpation on hearing sensitivity in *Ictalurus nebulosus* (bullhead catfish).

Frequency (Hz)	Loss in Sound Pressure Sensitivity (dB)	
	1	2
60		43
120		33
210	4	
254	6	
330	10	
400		40
410	11	
550	15	
750	19	
800		35
1000	23	
1300	27	
1500	30	
3000		49
6000		42

Notes:

The accepted name for the bullhead catfish is *Ictalurus nebulosus*. The names given in the titles of these papers (both spellings) are no longer used.

The malleus is the largest pair of the Weberian ossicles mechanically linking the swimbladder and the ear in Otophysan fishes.

1- Underwater sound source. Conditioned feeding response. Average of 4 operated animals (swimbladder mutilation) relative to average normal thresholds. No absolute sound level calibration.

2- The methods used were as described for Poggendorf (1952) in Fig. F2-0. The data shown here are the differences between the audiogram for animal A4 from Fig. F2-0 and the mean audiogram determined for 3 other animals after malleus extirpation.

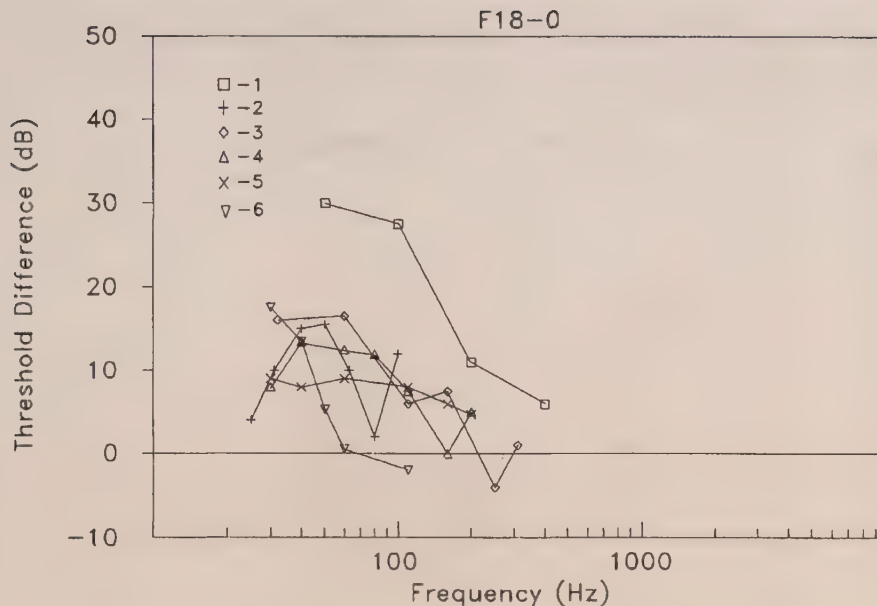


Fig. F18-0. Difference between sound pressure detection thresholds determined with underwater loudspeakers at different distances from the animal, as a function of frequency. The dB value plotted is the threshold at the greatest distance tested minus the threshold at the smallest distance tested.

- 1- *Carassius auratus* - goldfish (Enger, 1966)
- 2- *Heterodontus francisci* - horn shark (Kelly and Nelson, 1975)
- 3- *Salmo salar* - Atlantic salmon (Hawkins and Johnstone (1978)
- 4- *Pleuronectes platessa* - plaice (Chapman and Sand 1974)
- 5- *Limanda limanda* - dab (Chapman and Sand 1974)
- 6- *Gadus morhua* - cod (Chapman and Hawkins, 1973)

References:

- Chapman, C.J. and Hawkins, A.D. (1973) A field study of hearing in the cod, *Gadus morhua* L. J. Comp. Physiol. 85, 147-167.
- Chapman, C.J. and Sand, O. (1974) Field studies of hearing in two species of flatfish, *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). Comp. Biochem. Physiol. 47, 371-385.
- Enger, P.S. (1966) Acoustic threshold in goldfish and its relation to the sound source distance. Comp. Biochem. Physiol. 18, 859-868.
- Hawkins, A.D., Johnstone, A.D.F. (1978) The hearing of the Atlantic salmon, *Salmo salar*. J. Fish. Biol. 13, 655-673.
- Kelly, J.C., Nelson, D.R. (1975) Hearing thresholds of the horn shark, *Heterodontus francisci*. J. Acoust. Soc. Amer. 58, 905-909.

Table F18-0. Difference between sound pressure detection thresholds determined with underwater loudspeakers at different distances from the animal, as a function of frequency. The dB value plotted is the threshold at the greatest distance tested minus the threshold at the smallest distance tested.

Frequency (Hz)	Sound Pressure Sensitivity Difference (dB)					
	1	2	3	4	5	6
25		4				
30				8	9	17.5
31		10				
32			16			
40		15		13.5	8	13.5
50	30	15.5				5.3
60			16.5	12.5	9	0.5
63		10				
80		2		12		
100	27.5	12				
110			6	7.5	8	-2
160			7.5	0	6	
200	11			5	4.7	
250			-4			
310			1			
400	6					

Notes:

1- Sound source distance: 0.2 m - 2 m. Underwater sound projector (J9) in a trough-like tank. Classically conditioned feeding response using a descending method of limits. Means: N=6.

2- Sound source distance: 0.3 m - 0.6 m. Underwater sound projector (J9) in a large wood tank. Classical cardiac conditioning using the staircase psychophysical procedure. Both sound pressure and acoustic particle displacement were measured in this experiment. It is likely that these thresholds were masked by ambient noise at frequencies of 80 Hz and below. Means: N=4.

3- Sound source distance: 0.65 m - 2.7 m. Underwater sound projector (J9) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=5.

4-5 Sound source distance: 0.7 m - 3 m. Underwater sound projector (J9) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=1 for *P. platessa*, N=2 for *L. limanda*. These species lack a swimbladder.

6- Sound source distance: 0.5 m - 50 m. Underwater sound projector (J9) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=43.

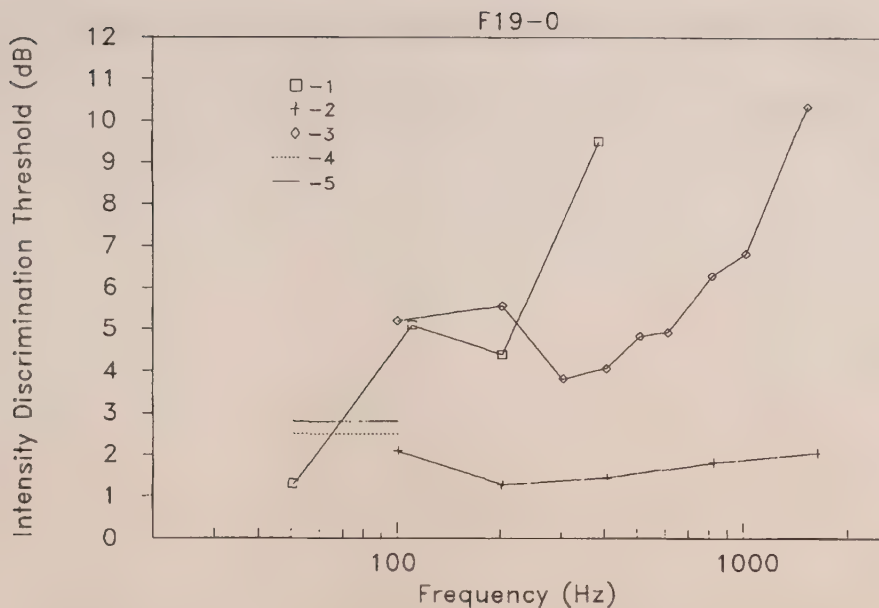


Fig. F19-0. Intensity discrimination thresholds as a function of frequency in several fish species.

- 1- *Gadus morhua* - cod, and *Melanogrammus aeglefinus* - haddock (Chapman and Johnstone, 1974)
- 2- *Carassius auratus* - goldfish (Fay, 1988)
- 3- *Carassius auratus* - goldfish (Jacobs and Tavalga, 1967)
- 4- *Carassius auratus* - goldfish (noise) (Hall, Patricoski and Fay, 1981)
- 5- *Carassius auratus* - goldfish (noise) (Fay, 1985)

References:

- Chapman, C.J. and Johnstone, A.D.F. (1974) Some auditory discrimination experiments on marine fish. *J. Exp. Biol.* 61, 521-528.
- Fay, R.R. (1985) Sound intensity processing by the goldfish. *J. Acoust. Soc. Amer.* 78, 1296-1309.
- Fay, R.R. (1988) Intensity discrimination of pulsed pure tones in the goldfish, *Carassius auratus*. *J. Acoust. Soc. Amer.* in press.
- Hall, L. Patricoski, M. Fay, R.R. (1981). Neurophysiological mechanisms of intensity discrimination in the goldfish. In W.N. Tavalga, A.N. Popper and R.R. Fay (eds), *Hearing and Sound Communication in Fishes*, Springer-Verlag: New York, pp. 179-186.
- Jacobs, D.W. and W.N. Tavalga. (1967) Acoustic intensity limens in the goldfish. *Anim. Behav.* 15, 324-335.

Table F19-0. Intensity discrimination thresholds as a function of frequency in several fish species.

Frequency (Hz)	Intensity Discrimination Threshold (dB)				
	1	2	3	4	5
50	1.3				
100		2.1	5.2		
110	5.1				
200	4.4	1.28	5.5		
300			3.82		
380	9.5				
400		1.44	4.06		
500			4.83		
600			4.93		
800		1.8	6.29		
1000			6.82		
1500			10.34		
1600		2.02			
Noise				2.5	2.8

Notes:

Intensity discrimination thresholds are determined by conditioning the animals to detect a change from ongoing sound bursts of a standard intensity to a sequence of bursts of different intensity. In 1, 2, and 4, each burst in the conditioned stimulus (CS) was presented with the same intensity increment above the standard. In 3, the bursts of the CS alternated between the standard intensity and the incremented intensity. In 5, the CS consisted of sinusoidal amplitude modulation (SAM) impressed on a continuous noise.

1- A pulsed tone was switched between two different sound projectors. Similar data (not shown) were also obtained by amplitude modulating a continuous tone at about 2 Hz.

Underwater sound projector (J9) at 3 meters in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Sound levels from 0 to 10 dB. Sound pulses 500 msec in duration, 75 msec rise/fall times, 1 sec inter pulse interval. Data are medians from pooled thresholds from 3 cod and 1 haddock.

2- Underwater loudspeaker. Classical respiratory conditioning using the staircase psychophysical procedure. Sound pulses were 500 msec, 20 msec rise/fall times, at 45 dB sensation level with 1 sec inter pulse interval. Thresholds at 25 dB sensation level (not shown here) were about 0.6 dB higher than those at 45 dB. Means: N=4.

3- Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Sound pulses 1 sec in duration, 160 msec inter pulse interval. Most data obtained at an overall intensity of from -20 to 0 dB re: 1 dyne cm⁻². Means: N=12.

4- Air loudspeaker. Classical respiratory conditioning using the staircase psychophysical procedure. Determined in the same acoustical set-up used in F31-0 to F33-0. Detection of 2.5 Hz sinusoidal amplitude modulation (SAM) impressed on continuous noise at 25-35 dB sensation level. The intensity discrimination threshold is defined as the level difference, in dB, between the peak and the trough of the SAM envelope at threshold. Means: N=4.

5- Same as #2 except that the signal was broad band noise.

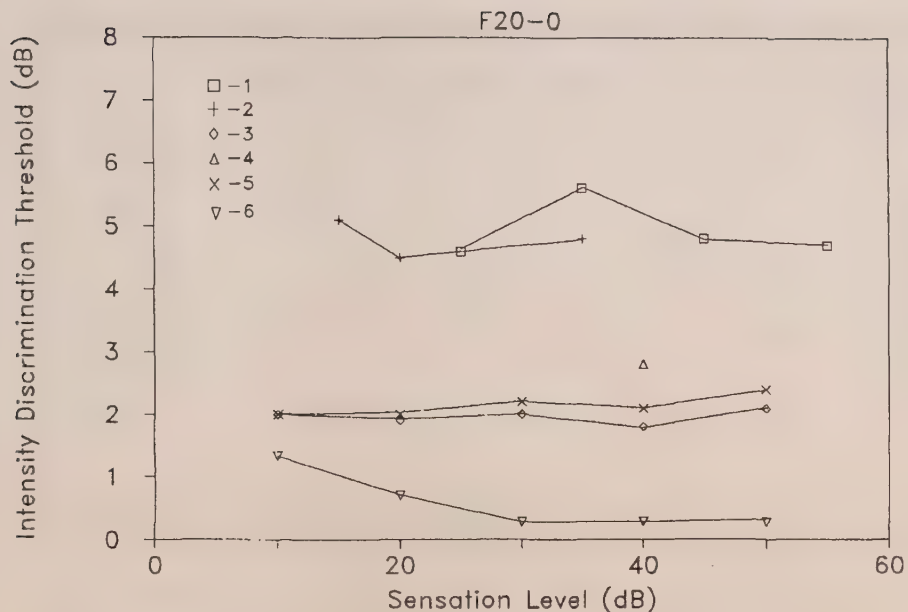


Fig. F20-0. Intensity discrimination thresholds as a function of sound intensity.

- 1- *Carassius auratus* - goldfish, pulsed tone (Jacobs and Tavalga, 1967)
- 2- *Gadus morhua* - cod, and *Melanogrammus aeglefinus* - haddock, pulsed tone, (Chapman and Johnstone, 1974)
- 3- *Carassius auratus* - goldfish, pulsed tone (Fay, 1985)
- 4- *Carassius auratus* - goldfish, pulsed noise (Fay, 1985)
- 5- *Carassius auratus* - goldfish, noise increment (Fay, 1985)
- 6- *Carassius auratus* - goldfish, tone increment (Fay, 1985)

References:

- Chapman, C.J. and Johnstone, A.D.F. (1974) Some auditory discrimination experiments on marine fish. *J. Exp. Biol.* 61, 521-528.
- Fay, R.R. (1985) Sound intensity processing by the goldfish. *J. Acoust. Soc. Amer.* 78, 1296-1309.
- Jacobs, D.W. and Tavalga, W.N. (1967) Acoustic intensity limens in the goldfish. *Anim. Behav.* 15, 324-335.

Table F20-0. Intensity discrimination thresholds as a function of sound intensity.

Level Above Threshold (dB)	Intensity Discrimination Threshold (dB)					
	1	2	3	4	5	6
10			2		2	1.33
15		5.1				
20		4.5	1.9		2	0.7
25	4.6					
30			2		2.2	0.3
35	5.6	4.8				
40			1.8	2.8	2.1	0.29
45	4.8					
50			2.1		2.4	0.28
55	4.7					

Notes:

1- Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. 500 Hz sound pulses 1 sec in duration, 160 msec inter pulse interval.

Means: N=12.

2- A pulsed tone was switched between two different sound projectors.

Underwater sound projector (J9) at 3 meters in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. 110 Hz sound pulses 500 msec in duration, 75 msec rise/fall times, 1 sec inter pulse interval. Data are medians from 2 cod and 1 haddock.

3- Underwater loudspeaker. Classical respiratory conditioning using the staircase psychophysical procedure. 800 Hz sound pulses of 500 msec duration, 20 msec rise/fall times, 1 sec inter pulse interval. Means: N=4.

4- Same as 3 except that signal was a pulsed noise.

5- Same as 3 except that signal was a 160 msec increment in a continuous noise.

6- Same as 3 except that signal was a 160 msec increment in a continuous 800 Hz tone.

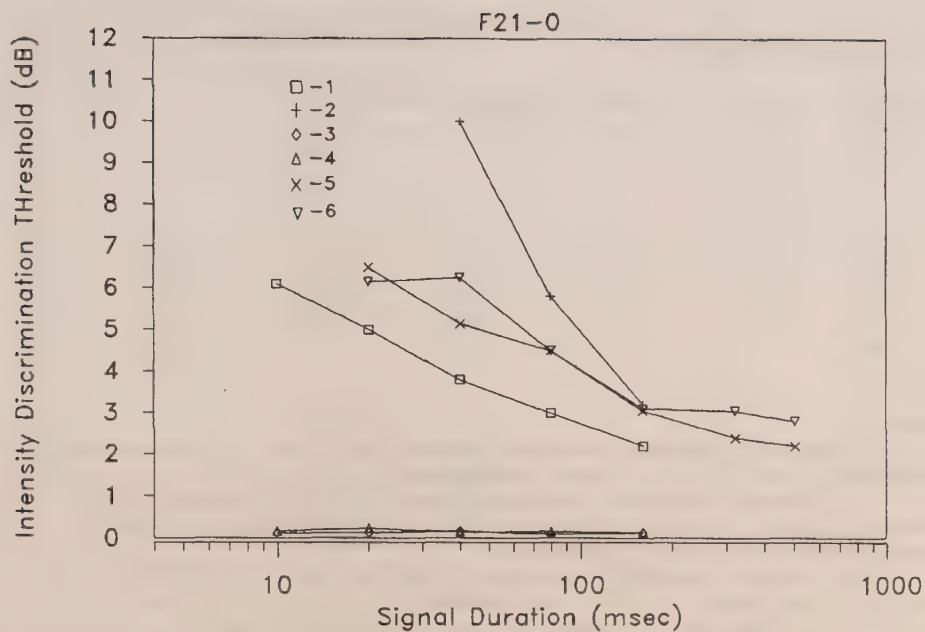


Fig. F21-0. Intensity discrimination threshold as a function of duration in *Carassius auratus* (goldfish).

- 1- Increment threshold in continuous noise.
- 2- Decrement (gap depth) threshold in continuous noise.
- 3- Increment threshold in a continuous 800 Hz tone
- 4- Decrement threshold in a continuous 800 Hz tone
- 5- Pulsed 800 Hz tone
- 6- Pulsed noise

Reference:

Fay, R.R. (1985) Sound intensity processing by the goldfish. *J. Acoust. Soc. Amer.* 78, 1296-1309.

Table F21-0. Intensity discrimination threshold as a function of duration in *Carassius auratus* (goldfish).

Signal Duration (msec)	Intensity Discrimination Threshold (dB)					
	1	2	3	4	5	6
10	6.1		0.12	0.17		
20	5		0.13	0.24	6.5	6.15
40	3.8	10	0.17	0.15	5.15	6.25
80	3	5.8	0.1	0.155	4.5	4.5
160	2.2	3.2	0.13	0.145	3.05	3.1
320					2.4	3.05
500					2.2	2.8

Notes:

Underwater loudspeaker in a small cylindrical water tank. Classical respiratory conditioning using the staircase psychophysical procedure. Means: N=4.

1- Increment thresholds in continuous broad band noise presented 40 dB SL (sensation level, or level above detection threshold). This function can be well fit with a power function having slope of -0.36.

2- Decrement thresholds in continuous broad band noise at 40 dB SL. This is a measure of the minimum detectable gap depth as a function of gap duration.

3- Increment thresholds on a continuous 800 Hz tone presented 40 dB SL.

4- Decrement thresholds on a continuous 800 Hz tone presented 40 dB SL.

5- Intensity discrimination thresholds for pulsed 800 Hz tone at 40 dB SL. This function can be well fit with a power function having slope of -0.35.

6- Intensity discrimination thresholds for pulsed noise presented at 40 dB SL. This function can be well fit with a power function having slope of -0.28.

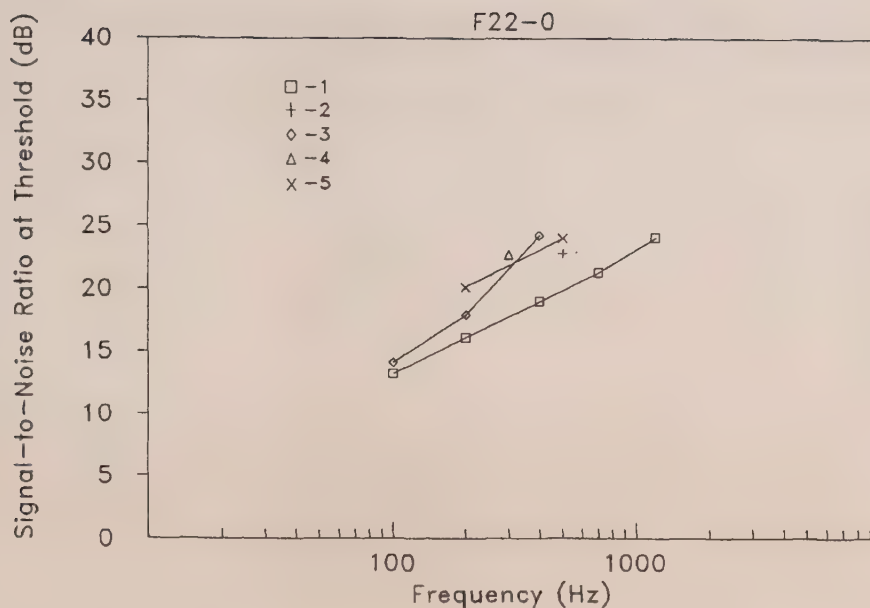


Fig. F22-0. Signal-to-noise ratios (in dB) at threshold for the detection of pure tones masked by broad band noise in several species.

- 1- *Carassius auratus* - goldfish (Fay, 1974)
- 2- *Carassius auratus* - goldfish (Tavolga, 1974)
- 3- *Arius felis* - marine catfish (Tavolga, 1982)
- 4- *Tilapia macrocephala* - African mouthbreeder (Tavolga, 1974)
- 5- *Lagodon rhomboides* - pinfish (Tavolga, 1974)

References:

- Fay, R.R. (1974) Masking of tones by noise for the goldfish (*Carassius auratus*). J. Comp. Physiol. Psych. 87, 708-716.
- Tavolga, W.N. (1974) Signal/noise ratio and the critical band in fishes. J. Acoust. Soc. Amer. 55, 1323-1333.
- Tavolga, W.N. (1982) Auditory acuity in the sea catfish (*Arius felis*). J. Exp. Biol. 96, 367- 376.

Table F22-0. Signal-to-noise ratios (in dB) at threshold for the detection of pure tones masked by broad band noise in several species.

Frequency (Hz)	Signal-to-Noise Ratio at Threshold (dB)				
	1	2	3	4	5
100	13.2		14.1		
200	16.1		17.9		20.1
300				22.7	
400	19		24.2		
500		22.8			24
700	21.3				
1200	24.1				

Notes:

In these experiments (and in the ones following in Figs. F23-0, F24-0, and F25-0), the detection thresholds for pure tones are obtained in the presence of broad band noise. The noise spectrum is known or presumed to be flat in the band surrounding the signal frequency, and noise level is given in dB/Hz (spectrum level). The signal-to-noise ratio is the level of the signal at threshold minus the spectrum level of the noise (both measures in dB). This has been termed the critical ratio, or CR. It has been interpreted as a measure of the frequency selectivity of the auditory system. The effective bandwidth of the hypothetical auditory filters used in signal detection can be estimated by raising 10 to the power CR/10. This value is known as the critical ratio bandwidth. Given that a receiver is operating in a noisy environment, the CR allows one to predict what signals will be detected simply by measuring ambient noise levels.

1- Air loudspeaker above a small laboratory water tank. Classical respiratory conditioning using the descending method of limits. Masking noise spectrum given. N=4.

2- Air loudspeaker. Instrumental avoidance conditioning using the staircase psychophysical procedure. S/N averaged over several masker bandwidths shown to be wider than the effective masking bandwidth. Means: N=10.

3- Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Means: N=10.

4- Air loudspeaker. Instrumental avoidance conditioning using the staircase psychophysical procedure. Means: N=10.

5- Air loudspeaker. Instrumental avoidance conditioning using the staircase psychophysical procedure. Means: N=6.

Other studies of the masking of tones by noise can be found in Cahn, Siler, and Wodinsky (1969), Cahn, Siler, and Auwarter (1970), and Buwalda (1981). These studies focused on the change in masking caused by manipulations of the wave impedance (ratio of pressure to particle velocity) of the signal tone and/or masker noise, and the results cannot be simply summarized in a figure or table without considerable explanation. In general, some of the results of these studies showed that there is a release from masking when the impedance of the signal differs from the impedance of the masker. This suggests different receptors detect signals of different impedance.

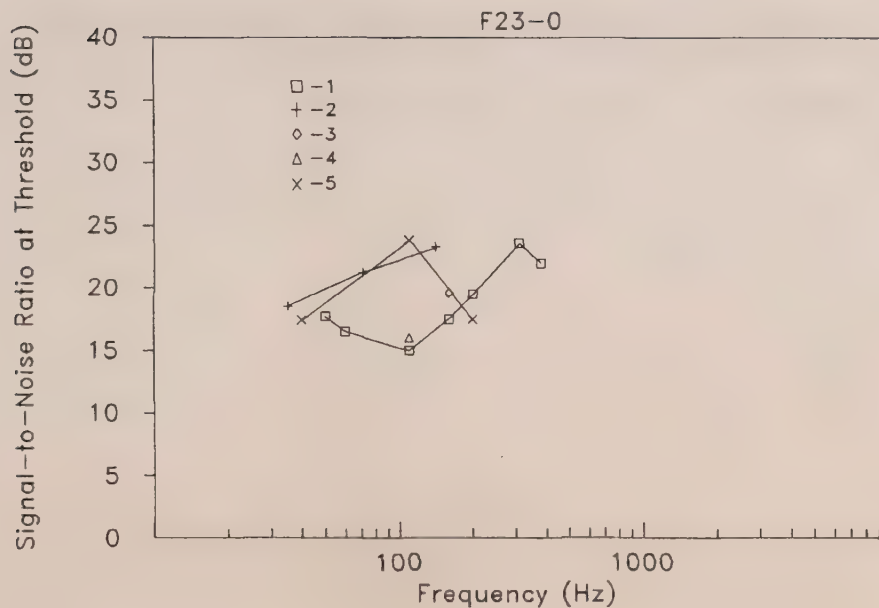


Fig. F23-0. Signal-to-noise ratios (in dB) at threshold for the detection of pure tones masked by broad band noise in *Gadus morhua* (cod).

- 1- Chapman and Hawkins, 1973
- 2- Buerkle, 1968
- 3- Chapman and Johnstone, 1974
- 4- Hawkins and Sand, 1977
- 5- Chapman, 1973

References:

- Buerkle, U. (1968) Relation of pure tone thresholds to background noise level in the Atlantic cod (*Gadus morhua*). J. Fish. Res. Bd. Canada 25, 1155-1160.
- Chapman, C.J. (1973) Field studies of hearing in teleost fish. Helgoländer wiss. Meeresunters. 24, 371-390.
- Chapman, C.J. and Hawkins, A.D. (1973) A field study of hearing in the cod, *Gadus morhua* L. J. Comp. Physiol. 85, 147-167.
- Chapman, C.J. and Johnstone, A.D.F. (1974) Some auditory discrimination experiments on marine fish. J. Exp. Biol. 61, 521-528.
- Hawkins, A.D. and Sand, O. (1977) Directional hearing in the median vertical plane by the cod. J. Comp. Physiol. 122, 1-8.

Table F23-0. Signal-to-noise ratios (in dB) at threshold for the detection of pure tones masked by broad band noise in *Gadus morhua* (cod).

Frequency (Hz)	Signal-to-Noise Ratio at Threshold (dB)				
	1	2	3	4	5
35.3		18.5			
40					17.4
50	17.7				
60	16.5				
70.7		21.2			
110	15			16	23.8
141		23.3			
160	17.5		19.6		
200	19.5				17.5
310	23.6				
380	22				

Notes:

1- Underwater sound projector (J9) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical method. The noise levels occurring in the free field were measured during all absolute threshold determinations (Fig. F6-0), and those conditions showing a good correlation between noise level and threshold were used in calculating the S/Ns shown here. Means: N=43.

2- Underwater loudspeaker (J9) in concrete tank. Classical cardiac conditioning using descending method of limits. Means: N=8.

3- Underwater projector (J9) in an acoustic free field. Classical cardiac conditioning using the descending method of limits. Data combined for 9 cod and 3 haddock, and averaged over pure tone frequencies of 60-380 Hz (plotted at 150 Hz).

4- Underwater projector (J9) in an acoustic free field. Classical cardiac conditioning using staircase psychophysical procedure. Means: N=3.

5- Same as for #4, above. Means: N=3.

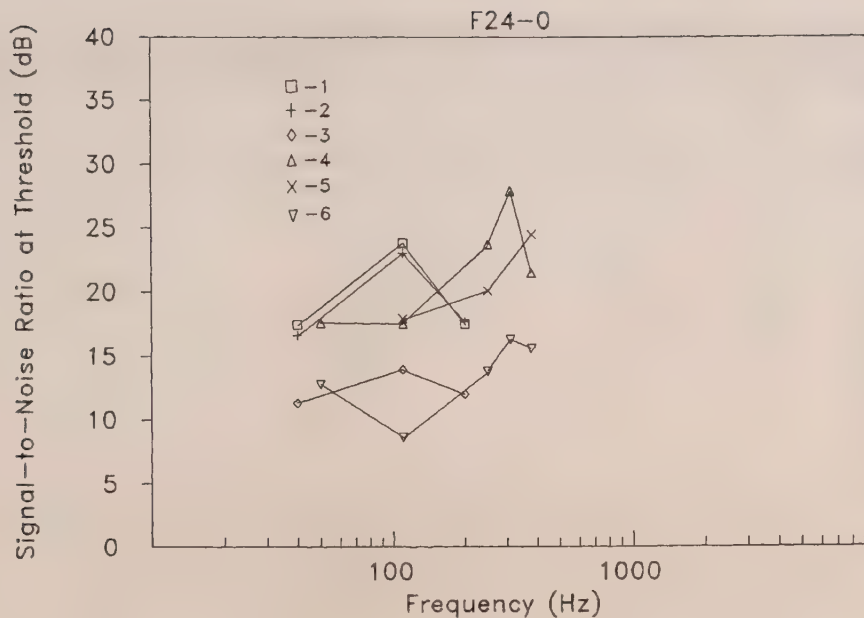


Fig. F24-0. Signal-to-noise ratios (in dB) at threshold for the detection of pure tones masked by broad band noise in the cod and the haddock for different angular separations between the tone signal source and noise masker source.

- 1- 0 degrees angular separation
- 2- 10 degrees angular separation
- 3- 85 degrees angular separation
- Gadus morhua* - cod (Chapman, 1973)
- 4- 0 degrees angular separation
- 5- 10 degrees angular separation
- 6- 85 degrees angular separation
- Melanogrammus aeglefinus* - haddock (Chapman, 1973)

Reference:

Chapman, C.J. (1973) Field studies of hearing in teleost fish. *Helgoländer wiss. Meeresunters.* 24, 371-390.

Table F24-0. Signal-to-noise ratios (in dB) at threshold for the detection of pure tones masked by broad band noise in the cod and the haddock for different angular separations between the tone signal source and noise masker source.

Frequency (Hz)	Signal-to-Noise Ratio at Threshold (dB)					
	1	2	3	4	5	6
40	17.4	16.6	11.3			
50				17.6		12.8
110	23.8	23	13.9	17.5	17.9	8.6
200	17.5	17.7	12			
250				23.7	20.1	13.8
310				27.9		16.3
380				21.5	24.5	15.6

Notes:

This experiment asks whether the spatial location of a noise source relative to a signal source has an effect on the effectiveness of the noise to mask the detection of the signal. The results plotted here (see also Fig. F25-0) show that for both species tested, the S/N at threshold declines by 7 dB or so when the signal and noise sources are separated in azimuth by 85 degrees. The effect is similar at all the frequencies tested. This means that the auditory system of these animals are "spatial" filters, and that the ambient noise effective in masking a signal is restricted to that received from the general direction of the signal. This is part of the definition of "directional hearing" and has likely been selected for throughout the evolution of hearing as a strategy to gain sensitivity in an omnidirectional noise field.

In man, this directional masking effect is referred to as the "cocktail party effect." It is a common observation that those with a hearing loss in one ear, and thus an impairment in the ability to hear directionally, tend to avoid cocktail parties or other similar gatherings. The reason is that at typical cocktail parties, speech signals are usually near the threshold for recognition in a background of intense, omnidirectional noise. Any reduction in the ability to reject some of this noise makes such speech difficult if not impossible to hear, and the party a frustrating waste of time.

Underwater sound projectors in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=3 for *Gadus morhua*, N=2 for *Melanogrammus aeglefinus*.

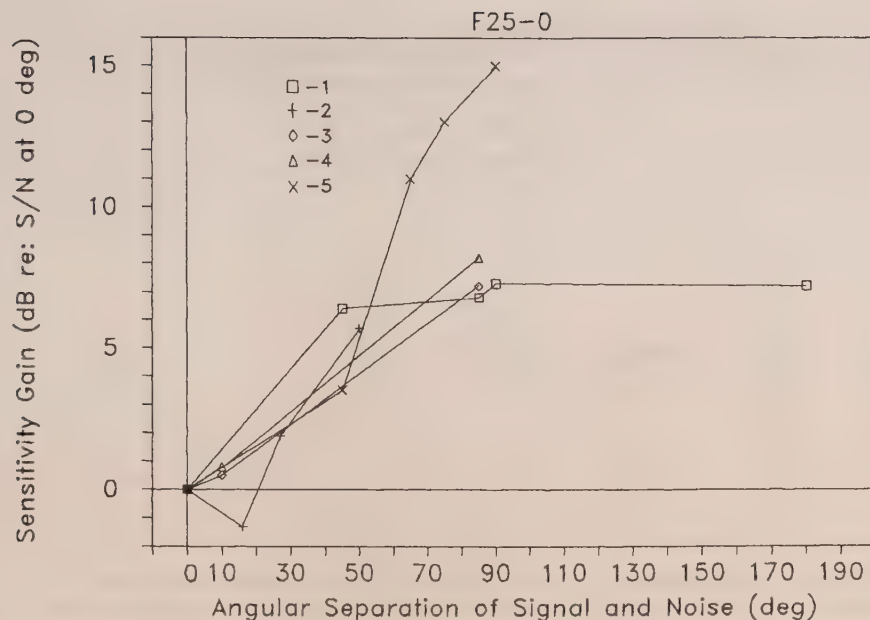


Fig. F25-0. The difference (in dB) between the S/N for a pure tone masked by a broad band noise at 0° azimuth and elevation, and the S/N obtained when the noise was displaced in azimuth or elevation by the indicated angle.

- 1- *Gadus morhua* - cod (Chapman and Johnstone, 1974)
Melanogrammus aeglefinus - haddock
- 2- *Gadus morhua* - cod (Hawkins and Sand, 1977)
- 3- *Gadus morhua* - cod (Chapman, 1973)
- 4- *Melanogrammus aeglefinus* - haddock (Chapman, 1973)
- 5- *Gadus morhua* - cod (Buwalda, 1981)

References:

- Buwalda, R.J.A. (1981) Segregation of directional and nondirectional acoustic information in the cod. In W.N. Tavolga, A.N. Popper, and R.R. Fay (eds), *Hearing and Sound Communication in Fishes*. Springer-Verlag: New York, pp. 139-178.
- Chapman, C. J. (1973) Field studies of hearing in teleost fish. *Helgoländer wiss. Meeresunters.* 24, 371-390.
- Chapman, C. J. and Johnstone, A. D. F. (1974) Some auditory discrimination experiments on marine fish. *J. Exp. Biol.* 61, 521-528.
- Hawkins, A. D. and Sand, O. (1977) Directional hearing in the median vertical plane by the cod. *J. Comp. Physiol.* 122, 1-8.

Table F25-0. The difference between the S/N for a pure tone masked by a broad band noise at 0° azimuth and elevation, and the S/N obtained when the noise was displaced in azimuth or elevation by the indicated angle.

Angle Between Signal and Noise Sources (Deg.)	Sensitivity Gain (dB re: S/N at 0°)				
	1	2	3	4	5
0	0	0	0	0	0
10			0.5	0.8	
16		-1.3			
27		1.9			
45	6.4				3.5
50		5.7			
65					11
75					13
85	6.8		7.2	8.2	
90	7.3				15
180	7.2				

Notes:

This is a clear indication of the "cocktail party effect" in two fish species, demonstrated in both azimuth (1,3,4,5) and elevation (2). Most authors agree that the basis for this directional filtering is the directional sensitivity of the hair cells as they are arrayed on the macular surfaces, and that the axis of acoustic particle motion must be represented in the pattern of activity across many neural channels with different directional orientations.

1- This experiment presents an interesting data point at a signal to noise azimuthal separation of 180° showing the same advantage for signal detection observed at 90°. This means that the receiver must have some information about the direction of wave propagation as well as about the axis of acoustic particle motion.

Underwater sound projector in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=9 for *G. morhua* and N=3 for *M. aeglefinus*. Data averaged over species and over signal frequencies of from 60 to 380 Hz. Noise source displaced in azimuth.

2- In this experiment, the noise source was displaced in elevation. These data show that directional hearing in the cod is as acute in elevation as it is in azimuth.

Underwater sound projector (J9) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure.

3-4 Underwater sound projector (J9) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. For *G. morhua* (Means: N=3) and *M. aeglefinus* (Means: N=2), these are the data plotted in F24-0 for Chapman (1973), averaged across frequencies. Noise source displaced in azimuth.

5- Classical cardiac conditioning using the staircase psychophysical procedure. Experiments were carried out in the laboratory using a three-dimensionally synthesized sound field (three orthogonal pairs of underwater loudspeakers) in which the impedance of the sound field in the region of the fish (the ratio of pressure to particle velocity) could be manipulated over a wide range. The signal was a 105 Hz tone presented at a very low pressure-to-velocity ratio (large motional component compared with the far field case). The noise was wide band with low pressure-to-velocity ratio. The azimuth of noise particle motion could be manipulated precisely in the synthesized sound field. Thresholds for noise to the left and right of 0° azimuth averaged here. N=2.

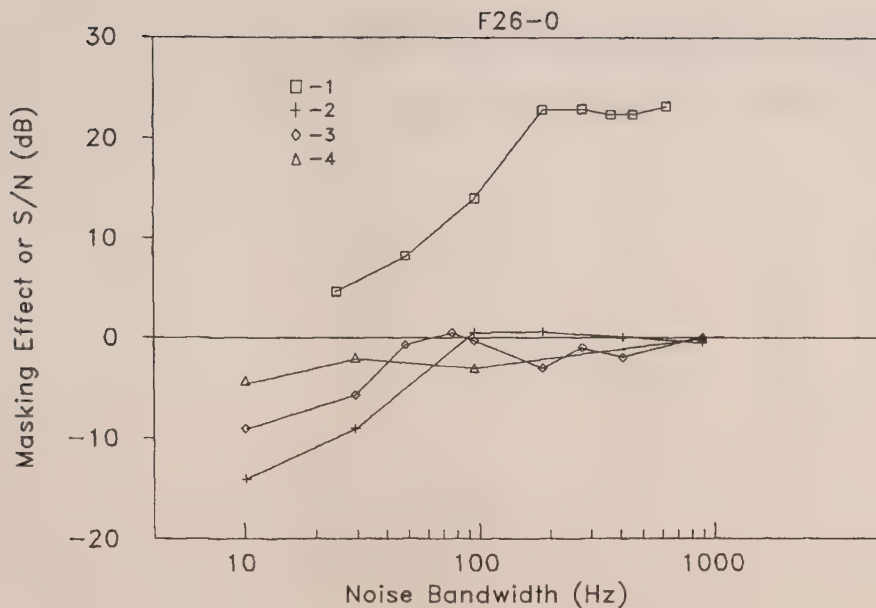


Fig. F26-0. Critical bands in fishes. The effect of noise masker bandwidth on the detection of pure tones centered in the masking bands.

- 1- Signal frequency= 500 Hz
Carassius auratus - goldfish (Tavolga, 1974)
- 2- Signal frequency= 380 Hz
- 3- Signal frequency= 160 Hz
- 4- Signal frequency= 60 Hz
Gadus morhua - cod (Hawkins and Chapman, 1975)

References:

- Hawkins, A.D. and Chapman, C.J. (1975) Masked auditory thresholds in the cod, *Gadus morhua* L. J. Comp. Physiol. 103, 209-226.
- Tavolga, W.N. (1974) Signal/noise ratio and the critical band in fishes. J. Acoust. Soc. Amer. 55, 1323-1333.

Table F26-0. Critical Bands in fishes. The effect of noise masker bandwidth on the detection of pure tones centered in the masking bands.

Bandwidth (Hz)	S/N at Threshold or Relative Masking Effect (dB)			
	1	2	3	4
10		-14	-9	-4.3
25	4.6			
30		-9	-5.7	-2
50	8.2		-0.7	
80			0.5	
100	14	0.5	-0.3	-3
200	22.8	0.6	-3	
300	22.9		-1	
400	22.4			
450		0	-2	
500	22.4			
700	23.2			
1000		-0.5	0	0

Notes:

The thresholds plotted for the goldfish (#1) are signal-to-noise ratios in dB, and those plotted for the cod (#2-4) are the masking effects of the designated bandwidths with respect to the masking effect for wide band noise.

The form of these functions is qualitatively similar to those determined similarly for humans and other vertebrates, and are consistent with the notion of a critical bandwidth phenomenon in fishes. This type of behavior would be expected from any system comprised of filters used in signal detection. The critical bandwidths derived from these functions are: 1: 200 Hz; 2: 30-100 Hz; 3: 30-50 Hz; 4: indeterminate.

1- Loudspeaker in air. Instrumental avoidance using the staircase psychophysical procedure. Means: N=10.

In this experiment, overall sound pressure level was held constant and spectrum level declined as the bandwidth was widened. This means that the signal remained at the same detectability at all subcritical bandwidths and that the ratio between signal level and noise spectrum level at threshold therefore increased until the noise bandwidth became supercritical.

2-4- Underwater loudspeaker (J9) at 2m from the fish in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=12.

In this experiment, spectrum level of the noise was held constant as the masker bandwidth was reduced from very wide band (supercritical) to the lowest subcritical bands used. The "masking effect" tabled and plotted is the reduction in threshold caused by narrowing the masker band, with reference to the threshold in the wide band condition.

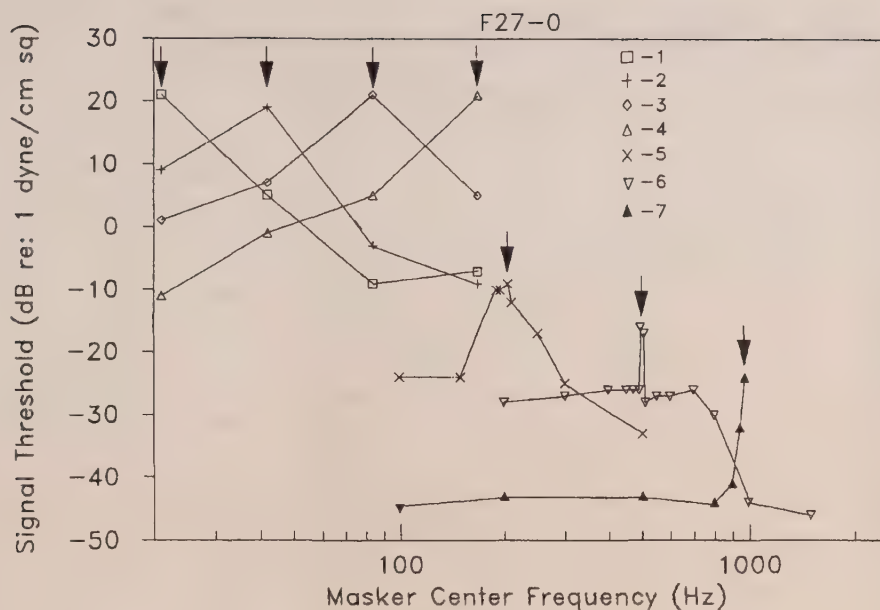


Fig. F27-0. Auditory filter shapes in two fish species. Thresholds for the detection of tones or narrow band noise as a function of masker frequency.

1- Signal: 21 Hz, Masker: 10 dB re: 1 dyne cm⁻²

2- 42 Hz, 10 dB

3- 84 Hz, 10 dB

4- 168 Hz, 10 dB

Gadus morhua, cod (Buerkle, 1969)

5- Signal: 200 Hz, Masker: 0 dB re: 1 dyne cm⁻²

6- 500 Hz, 0 dB

7- 1k Hz, 0 dB

Carassius auratus, goldfish (Tavolga, 1974)

References:

Buerkle, U. (1969) Auditory masking and the critical band in Atlantic cod

(*Gadus morhua*). J. Fish. Res. Bd. Canada 26, 1113-1119.

Tavolga, W.N. (1974) Signal/noise ratio and the critical band in fishes. J. Acoust.

Soc. Amer. 55, 1323-1333.

Table F27-0. Auditory filter shapes in two fish species. Thresholds for the detection of tones or narrow band noise as a function of masker frequency.

Masker Frequency (Hz)	Signal Detection Threshold (dB re: 1 dyne cm ⁻²)						
	1	2	3	4	5	6	7
21	21	9	1	-11			
42	5	19	7	-1			
84	-9	-3	21	5			
100					-24	-45	
150					-24		
168	-7	-9	5	21			
190					-10		
195					-10		
200						-28	-43
205					-9		
210					-12		
250					-17		
300					-25	-27	
400						-26	
450						-26	
470						-26	
490						-26	
495						-16	
500					-33		-43
505						-17	
510						-28	
550						-27	
600						-27	
700						-26	
800						-30	-44
900							-41
950							-32
980							-24
1000						-44	
1500						-46	

Notes:

Arrows locate signal frequency for each masking function.

1-4- Underwater loudspeaker (J9) in a large concrete tank. Classical cardiac conditioning using the ascending method of limits. Means: N=15.

Half-octave noise bands served as signals and maskers. Masker frequency refers to the center frequency of the half-octave bands.

5-7- Air loudspeaker. Instrumental avoidance conditioning using the staircase psychophysical procedure. Means: N=10.

Pure tones served as maskers and signals. Note that thresholds are not shown for the cases in which signal and masker frequency were equal.

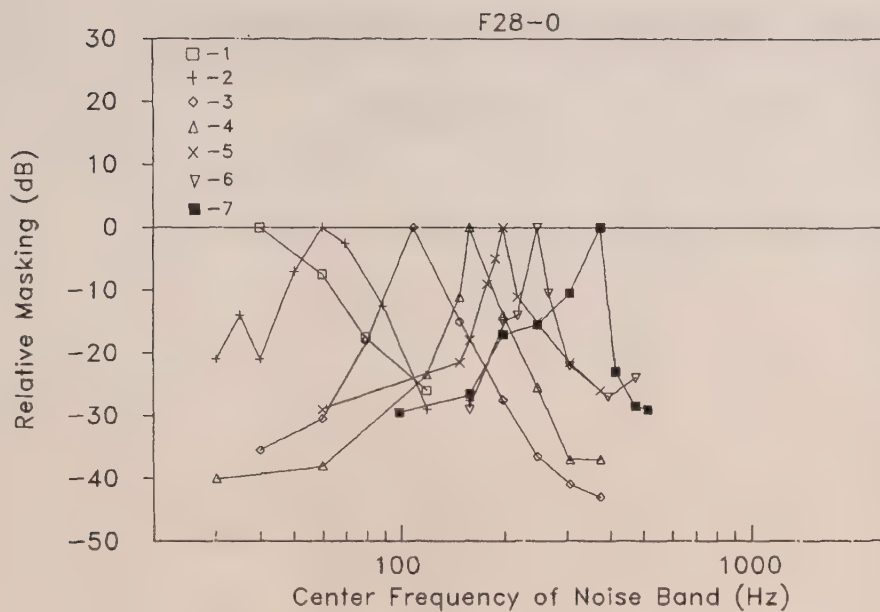


Fig. F28-0. Auditory filter shapes in *Gadus morhua* (cod) determined by masking.

- 1- Signal= 40 Hz
- 2- 60 Hz
- 3- 110 Hz
- 4- 160 Hz
- 5- 200 Hz
- 6- 250 Hz
- 7- 380 Hz

Reference:

Hawkins, A.D. and Chapman, C.J. (1975) Masked auditory thresholds in the cod, *Gadus morhua* L. J. Comp. Physiol. 103, 209-226.

Table F28-0. Auditory filter shapes in *Gadus morhua* (cod) determined by masking.

Masker Center Frequency (Hz)	Relative Masking (dB)						
	1	2	3	4	5	6	7
30		-21		-40			
35		-14					
40	0	-21	-35.5				
50		-7					
60	-7.5	0	-30.5	-38	-29		
70		-2.5					
80	-17.5		-18				
90		-12.5					
100							-29.5
110			0				
120	-26	-29		-23.5			
150			-15	-11	-21.5		
160		-27.5		0	-18	-29	-26.5
180					-9		
190					-5		
200			-27.5	-14	0	-15	-17
220					-11	-14	
250			-36.5	-25.5	-15	0	-15.5
270						-10.5	
310			-41	-37	-21.5	-22	-10.5
380			-43	-37	-26		0
400						-27	
420							-23
480						-24	-28.5
520							-29

Notes:

Signals were pure tones and maskers were 10 Hz-wide noise bands centered on the indicated frequencies. Signal frequency was fixed, and threshold signal level was determined as a function of masker center frequency. An additional masking function determined using tone maskers at a signal frequency of 160 Hz showed considerably sharper tuning than the same function determined using a noise masker. The authors attributed the difference to the existence of prominent beats in the tone masking condition.

These functions are remarkable in showing considerably sharper tuning than would be expected based on tuning curves for saccular nerve fibers in the cod (Horner, Hawkins, and Fraser, 1981).

Underwater loudspeaker (J9) in a free acoustic field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=12.

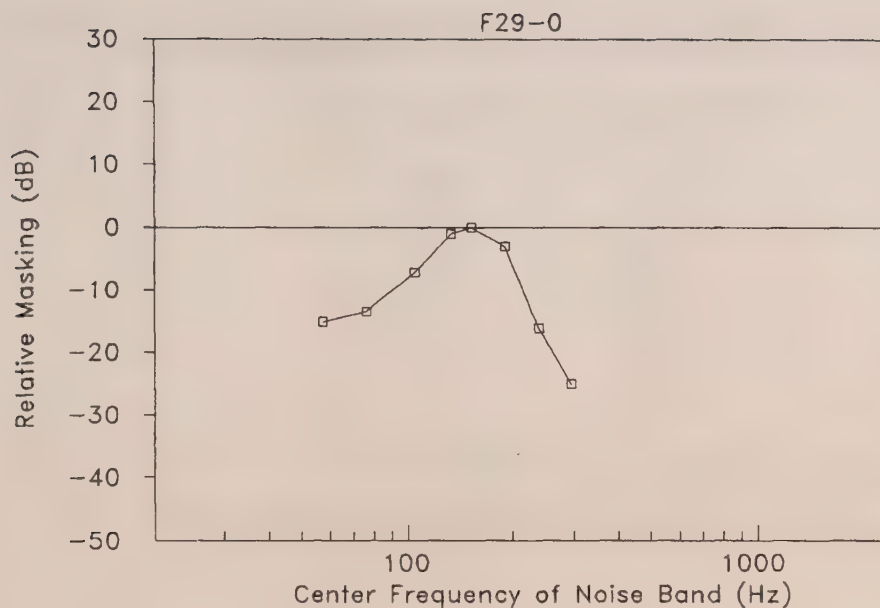


Fig. F29-0. Auditory filter shape for the Atlantic salmon, *Salmo salar*. A 160 Hz tone was masked by 10 Hz-wide noise bands at the indicated center frequencies.

Reference:

Hawkins, A.D., Johnstone, A.D.F. (1978) The hearing of the Atlantic salmon, *Salmo salar*. J. Fish. Biol. 13, 655-673.

Table F29-0. Auditory filter shape for the atlantic salmon, *Salmo salar*. A 160 Hz tone was masked by 10 Hz-wide noise bands at the indicated center frequencies.

Masker Center Frequency (Hz)	Relative Masking (dB)
60	-15.2
80	-13.5
110	-7.2
140	-1
160	0
200	-3
250	-16.2
310	-25

Notes:

Signal to be detected was a 160 Hz pure tone, and maskers were 10 Hz-wide noise bands of fixed intensity (not given).

Underwater loudspeaker (J9 or J11) in an acoustic free field. Classical cardiac conditioning using the staircase psychophysical procedure. Means: N=5.

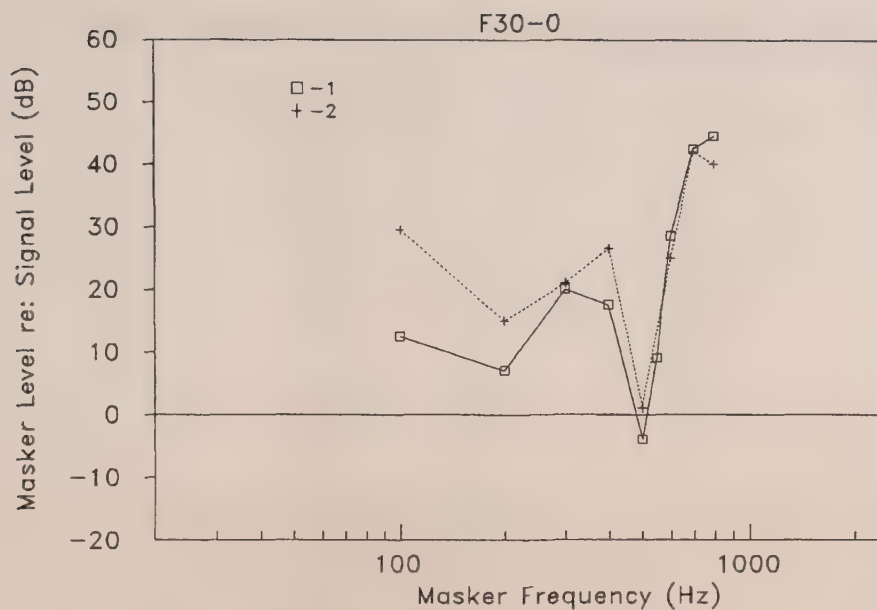


Fig. F30-0. Psychophysical tuning curves for *Gnathonemus petersii* (elephant nose) in forward and simultaneous masking.

- 1- Signal= 500 Hz in simultaneous masking
- 2- Signal= 500 Hz in forward masking (dashed line) ---

Reference:

McCormick, C.A. and Popper, A.N. (1984) Auditory sensitivity and psychophysical tuning curves in the elephant nose fish, *Gnathonemus petersii*. J. Comp. Physiol. 155, 753-761.

Table F30-0. Psychophysical tuning curves for *Gnathonemus petersii* (elephant nose) in forward and simultaneous masking.

Masker Frequency (Hz)	Masker Level re: Signal Level (dB)	
	1	2
100	12.5	29.5
200	7	15
300	20	21
400	17.5	26.5
500	-4	1
550	9	
600	28.5	25
700	42.4	42
800	44.5	40

Notes:

The psychophysical tuning curve (PTC) paradigm is designed to reveal the frequency selectivity of peripheral channels in the auditory system by mimicking the neurophysiological tuning curve paradigm. The signal to be detected is fixed at a level just above absolute threshold (usually about 10 dB above threshold), and the masker level at which signal detection is "just masked" is determined. The fixed signal tends to restrict the detection channels to those most sensitive to the signal near the quiet threshold. The curves show frequency selectivity in terms of the masking effect.

Simultaneous masking refers to the condition in which the signal is presented during the masker. Forward masking refers to the case in which a brief signal follows a masker in time. In this case, the masking effect persists after masker offset. Forward masking is likely caused, at least in part, by adaptation occurring at the hair cell-nerve fiber synapse. Forward masking is sometimes used to avoid certain interactions between signal and masker waveforms, such as beats, when presented simultaneously. In humans, PTCs are more sharply tuned in forward than in simultaneous masking (see C13-0). The origins of this effect are controversial.

Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Means: N=3. Signals and maskers were pure tones. Masker duration= 600 msec, signal duration= 40 msec, 5 msec rise/fall times, masker-signal interval=5 msec.

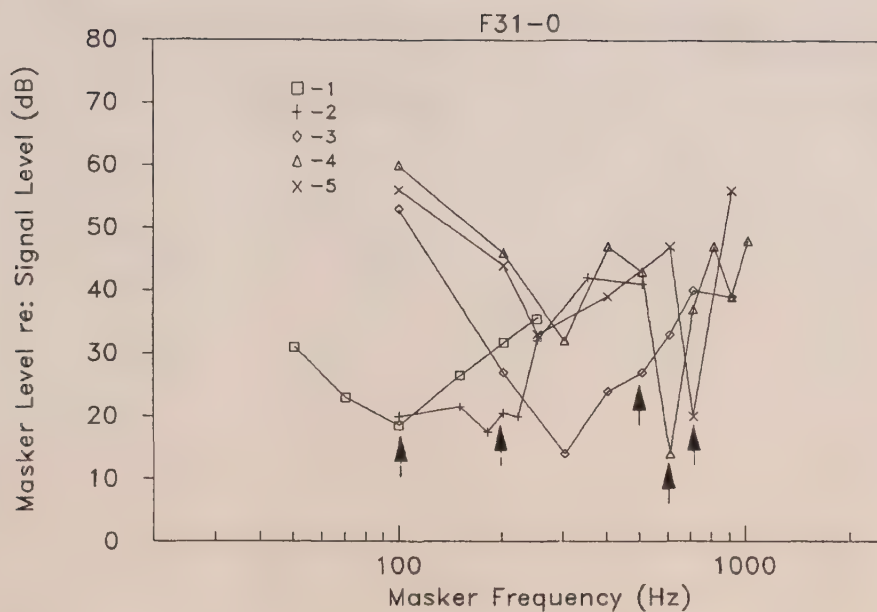


Fig. F31-0. Psychophysical tuning curves for *Carassius auratus* (goldfish) in simultaneous masking.

- 1- Signal = 100 Hz
- 2- 200 Hz
- 3- 500 Hz
- 4- 600 Hz
- 5- 700 Hz

Reference:

Fay, R.R., Ahroon, W., and Orawski, A. (1978) Auditory masking patterns in the goldfish (*Carassius auratus*): Psychophysical tuning curves. *J. Exp. Biol.* 74, 83-100.

Table F31-0. Psychophysical tuning curves for *Carassius auratus* (goldfish) in simultaneous masking.

Masker Center Frequency (Hz)	Masker level at Threshold re: Signal Level (dB)				
	1	2	3	4	5
50	31				
70	23				
100	18.5	20	53	60	56
150	26.5	21.5			
180		17.5			
200	31.7	20.5	27	46	44
220		20			
250	35.5	32			33
300			14	32	
350		42			
400			24	47	39
500		41	27	43	
600			33	14	47
700			40	37	20
800				47	
900			39	39	56
1000				48	

Notes:

Signals were 40 Hz-wide noise bands centered on the frequencies indicated by arrows presented 15 dB above absolute detection threshold. Maskers were continuous pure tones. The data are median thresholds for four animals tested at each signal frequency.

Air loudspeaker. Classical respiratory conditioning using the descending method of limits. Means: N=4.

Here, and in Fig. F33-0, the very sharply peaked PTCs for signals above about 500 Hz are likely a result of the detection of beat-like phenomena produced when the signal and masker frequencies fell within about 200 Hz of each other. The fact that the goldfish is remarkably sensitive to such amplitude modulations is illustrated in Figs. F43-0 and F44-0.

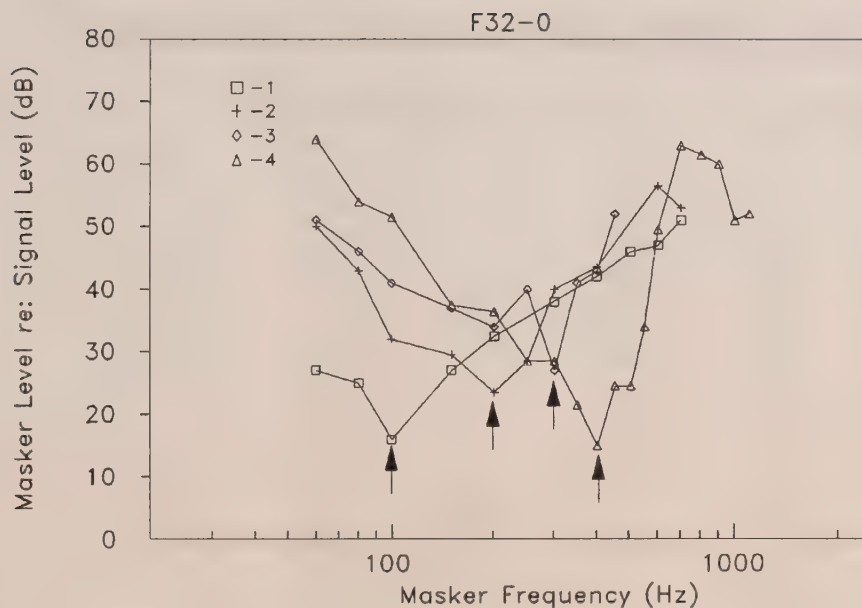


Fig. F32-0. Psychophysical tuning curves for *Carassius auratus* (goldfish) in simultaneous masking. Exp. 2.

- 1- Signal = 100 Hz
- 2- 200 Hz
- 3- 300 Hz
- 4- 400 Hz

Reference:

Fay, R.R., Ahroon, W., and Orawski, A. (1978) Auditory masking patterns in the goldfish (*Carassius auratus*): Psychophysical tuning curves. J. Exp. Biol. 74, 83-100.

Table F32-0. Psychophysical tuning curves for *Carassius auratus* (goldfish) in simultaneous masking. Exp. 2.

Masker Center Frequency (Hz)	Masker level at Threshold re: Signal Level (dB)			
	1	2	3	4
60	27	50	51	64
80	25	43	46	54
100	16	32	41	51.5
150	27	29.5	37	37.5
200	32.5	23.5	34	36.5
250		28.5	40	28.5
300	38	40	27	28.5
350			41	21.5
400	42	43.5	43	15
450			52	24.5
500	46			24.5
550				34
600	47	56.5		49.5
700	51	53		63
800				61.5
900				60
1000				51
1100				52

Notes:

The experimental conditions here were the same as in Fig. F31-0 except that the acoustic system was modified to have a smoother frequency response.

Signals were 40 Hz-wide noise bands centered on the frequencies indicated by arrows presented 15 dB above absolute detection threshold. Maskers were continuous pure tones. The data for #1-3 are median thresholds for two animals tested at each signal frequency, and the data for #4 are from one animal.

Air loudspeaker. Classical respiratory conditioning using the descending method of limits.

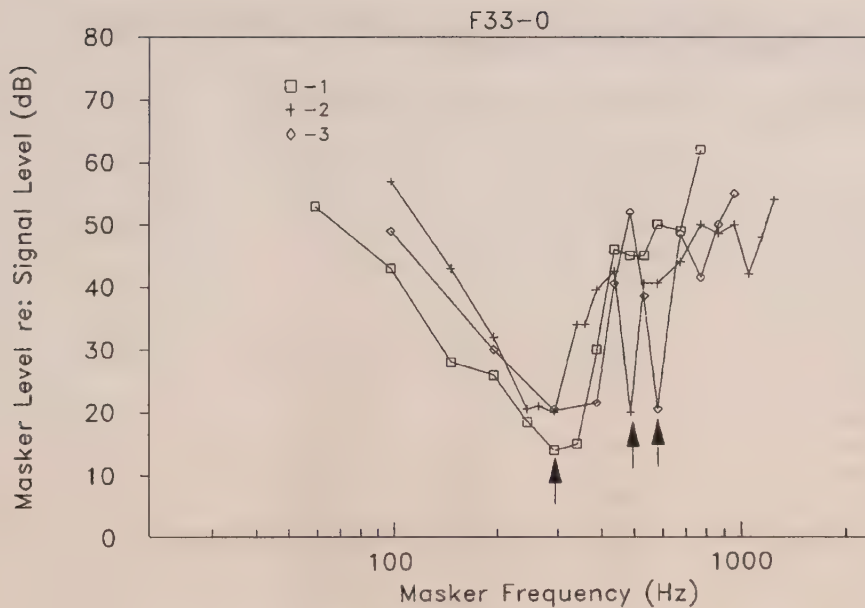


Fig. F33-0. Psychophysical tuning curves for *Carassius auratus* (goldfish) in simultaneous masking. Exp. 3 (pure tone signals).

- 1- Signal = 300 Hz
- 2- 500 Hz
- 3- 600 Hz

Reference:

Fay, R.R., Ahroon, W., and Orawski, A. (1978) Auditory masking patterns in the goldfish (*Carassius auratus*): Psychophysical tuning curves. J. Exp. Biol. 74, 83-100.

Table F33-0. Psychophysical tuning curves for *Carassius auratus* (goldfish) in simultaneous masking. Exp. 3 (pure tone signals).

Masker Center Frequency (Hz)	Masker level at Threshold re: Signal Level (dB)		
	1	2	3
60	53		
100	43	57	49
150	28	43	
200	26	32	30
250	18.5	20.5	
270		21	
300	14	20	20.5
350	15	34	
370		34	
400	30	39.5	21.5
450	46	42.5	40.5
500	45	20	52
550	45	40.5	38.5
600	50	40.5	20.5
700	49	44	48.5
800	62	50	41.5
900		48.5	50
1000		50	55
1100		42	
1200		48	
1300		54	

Notes:

These thresholds were determined in the same acoustic set-up as in Fig. F32-0.

Signals were pure tones at frequencies indicated by arrows presented 15 dB above absolute detection threshold. Maskers were continuous pure tones. The data for #1 are median thresholds for two animals tested, and the data for #2 and #3 are for one animal.

Air loudspeaker. Classical respiratory conditioning using the descending method of limits.

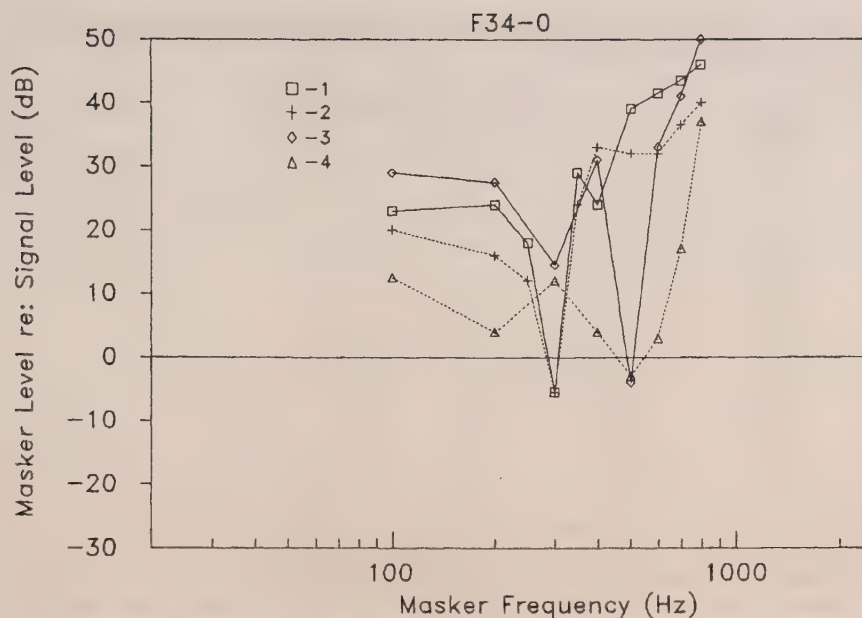


Fig. F34-0. Psychophysical tuning curves in simultaneous and forward masking in *Notopterus chitala* (clown knifefish).

Dashed lines indicate forward masking conditions.

- 1- Signal = 300 Hz; simultaneous masking
- 2- 300 Hz; forward
- 3- 500 Hz; simultaneous
- 4- 500 Hz; forward

Reference:

Coombs, S. and Popper, A.N. (1981) Comparative frequency selectivity in fishes: Simultaneously and forward-masked psychophysical tuning curves. *J. Acoust. Soc. Amer.* 71, 133-141.

Table F34-0. Psychophysical tuning curves in simultaneous and forward masking in *Notopterus chitala* (clown knifefish).

Masker Frequency (Hz)	Masker Level re: Signal Level at Threshold (dB)			
	1	2	3	4
100	23	20	29	12.5
200	24	16	27.5	4
250	18	12		
300	-5.5	-5.5	14.5	12
350	29	24		
400	24	33	31	4
500	39	32	-4	-3
600	41.5	32	33	3
700	43.5	36.5	41	17
800	46	40	50	37

Notes:

In this and in Fig. F30-0, there is generally more masking and broader tuning in forward masking compared with simultaneous masking. This is unlike the case in humans and other vertebrates which show sharper tuning in forward masking.

Signals and maskers were pure tones. Signal level was set at the lowest intensity for each animal which would maintain an 80% correct avoidance. Forward maskers were 555 msec in duration, 5 msec rise/fall times. Signals were 40 msec in duration with 5 msec rise/fall times. Signals gated on with the masker in simultaneous masking, and gated on 5 msec after masker offset in forward masking.

Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Data are mean PTCs, N=3.

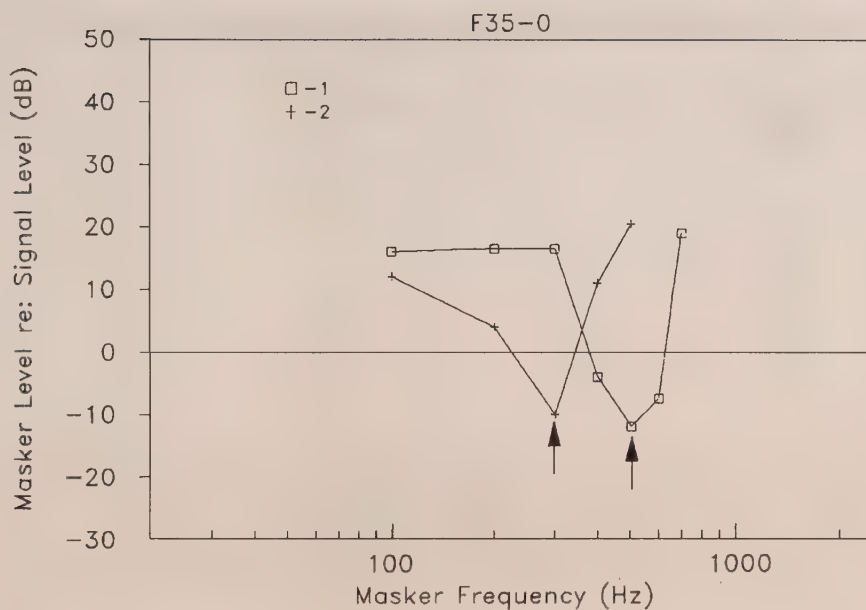


Fig. F35-0. Psychophysical tuning curves in simultaneous masking for two fish species.

- 1- *Osteoglossum bicirrhosum* - arawana
- 2- *Adioryx xantherythrus* - Hawaiian squirrelfish

Reference:

Coombs, S. and Popper, A.N. (1981) Comparative frequency selectivity in fishes: Simultaneously and forward-masked psychophysical tuning curves. *J. Acoust. Soc. Amer.* 71, 133-141.

Fig. F35-0. Psychophysical tuning curves in simultaneous masking for two fish species.

Masker Frequency (Hz)	Masker Level re: Signal Level at Threshold (dB)	
	1	2
100	16	12
200	16.5	4
300	16.5	-10
400	-4	11
500	-12	20.5
600	-7.5	
700	19	

Notes:

Signals and maskers were pure tones. Signal level was set at the lowest intensity for each animal which would maintain an 80% correct avoidance. Maskers were 600 msec in duration, 5 msec rise/fall times. Signals were 40 msec in duration with 5 msec rise/fall times. Signals gated on with the masker. Arrows indicate signal frequency.

Air loudspeaker. Instrumental avoidance using the staircase psychophysical procedure. Data for #1 are from one animal and data for #2 are medians from 3 animals.

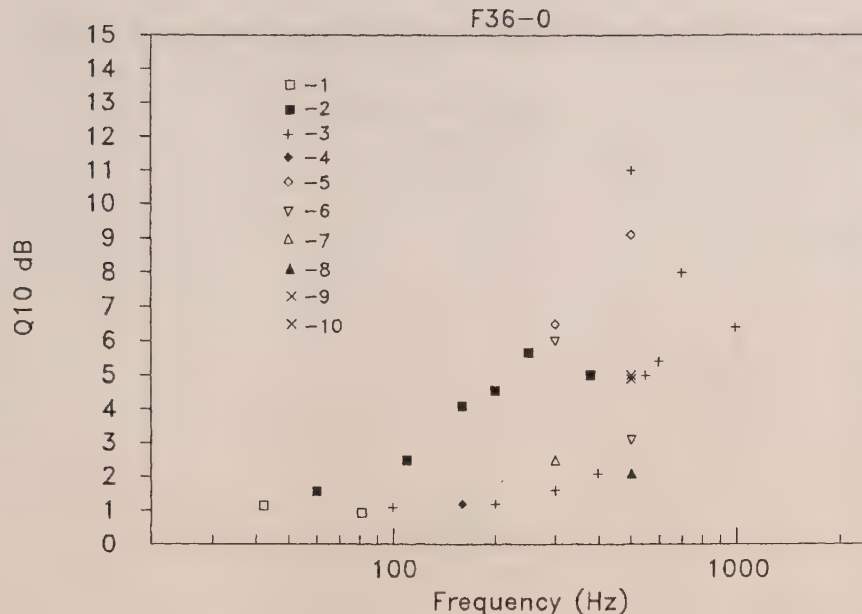


Fig. F36-0. The selectivity of auditory filters for seven fish species expressed in terms of Q_{10dB} .

- 1- *Gadus morhua* - cod (Buerkle, 1969)
- 2- *Gadus morhua* - cod (Hawkins and Chapman, 1975)
- 3- *Carassius auratus* - goldfish (Fay, Ahroon and Orawski, 1978)
- 4- *Salmo salar* - Atlantic salmon (Hawkins and Johnstone, 1978)
- 5- *Notopterus chitala* - clown knifefish (Coombs and Popper, 1982)
- 6- Same as 5, forward masking
- 7- *Adioryx xantherythrus* - Hawaiian squirrelfish (Coombs and Popper, 1982)
- 8- *Osteoglossum bicirrhosum* - arawana (Coombs and Popper, 1982)
- 9- *Gnathonemus petersii* - elephant nose (McCormick & Popper, 1984)
- 10- Same as 9, forward masking

References:

- Buerkle, U. (1969) Auditory masking and the critical band in Atlantic cod (*Gadus morhua*). J. Fish. Res. Bd. Canada 26, 1113-1119.
- Coombs, S. and Popper, A.N. (1981) Comparative frequency selectivity in fishes: Simultaneously and forward-masked psychophysical tuning curves. J. Acoust. Soc. Amer. 71, 133-141.
- Fay, R.R., Ahroon, W., and Orawski, A. (1978) Auditory masking patterns in the goldfish (*Carassius auratus*): Psychophysical tuning curves. J. Exp. Biol. 74, 83-100.
- Hawkins, A.D. and Chapman, C.J. (1975) Masked auditory thresholds in the cod, *Gadus morhua* L. J. Comp. Physiol. 103, 209-226.
- Hawkins, A.D., Johnstone, A.D.F. (1978) The hearing of the Atlantic salmon, *Salmo salar*. J. Fish. Biol. 13, 655-673.
- McCormick, C.A. and Popper, A.N. (1984) Auditory sensitivity and psychophysical tuning curves in the elephant nose fish, *Gnathonemus petersii*. J. Comp. Physiol. 155, 753-761.

Table F36-0. The selectivity of auditory filters for seven fish species expressed in terms of Q_{10dB} .

Frequency (Hz)	Frequency Selectivity Q_{10dB}									
	1	2	3	4	5	6	7	8	9	10
42	1.1									
60		1.6								
82	1.0									
100			1.1							
110		2.5								
160		4.1		1.2						
200		4.6	1.2							
250		5.7								
300			1.6		6.5	6	2.5			
380		5								
400			2.1							
500			11		9.1	3.1		2.1	5	5
550			5							
600			5.4							
700			8							
1000			6.4							

Notes:

The Q_{10dB} value is a measure of the selectivity of tuning defined as the center frequency of the filter function divided by the bandwidth (in Hz) 10 dB above the point of best sensitivity. The data presented here were taken from the papers whose data are displayed in Figs. F27-0 (cod only) through F35-0. See these figures for summaries of the experimental conditions. In some cases, Q_{10dB} values were determined graphically (#1,2,4). In others, the values were taken from tables presented in the papers cited (#5,6,7,8,9,10). In one case, the median Q_{10dB} was calculated from many values for individual animals presented graphically in the paper cited (#3).

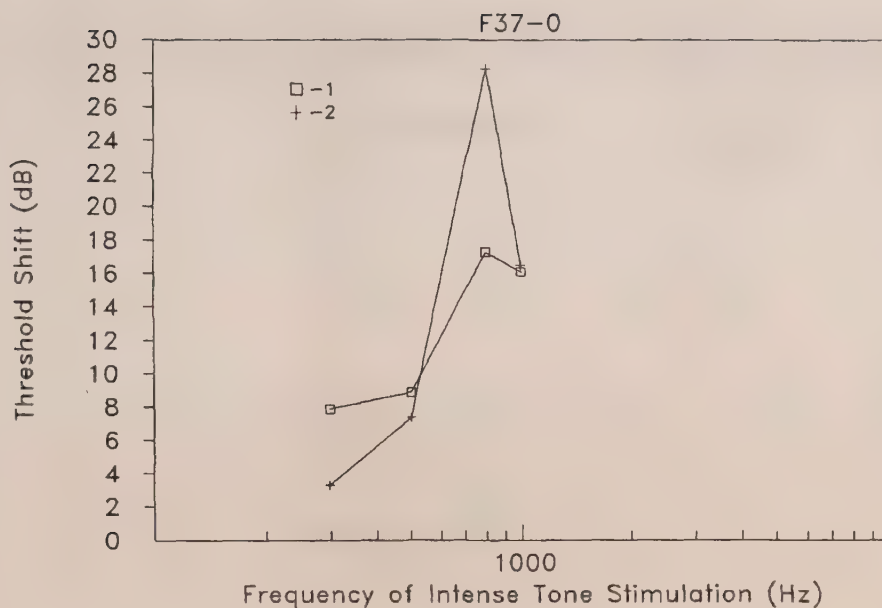


Fig. F37-0. The effect of prior intense tone stimulation on subsequent sound pressure detection thresholds at 500 Hz and 800 Hz in *Carassius auratus* (goldfish) (Popper and Clarke, 1976).

- 1- 500 Hz threshold
- 2- 800 Hz threshold

References:

Popper, A.N. and Clarke, N.L. (1976) The auditory system of the goldfish (*Carassius auratus*): Effects of intense acoustic stimulation. *Comp. Biochem. Physiol.* 53, 11-18.

Table F37-0. The effect of prior intense tone stimulation on subsequent sound pressure detection thresholds at 500 Hz and 800 Hz in *Carassius auratus* (goldfish) (Popper and Clarke, 1976).

Frequency of Intense Tone (Hz)	Threshold Shift (dB)	
	1	2
300	7.9	3.3
500	8.9	7.4
800	17.3	28.3
1000	16.1	16.5

Notes:

Air loudspeaker. Instrumental avoidance for some thresholds, and classical respiratory conditioning for other thresholds. The authors found no differences between thresholds obtained using the two different conditioning methods, so thresholds were pooled. The staircase psychophysical procedure was used. Means: N=25.

The intense stimuli were tones presented at 49 dB re: 1 dyne cm⁻² for 4 hours. Immediately following the intense tone stimulation, the threshold was measured for either a 500 Hz or 800 Hz tone in quiet. This determination required about 2 hours of testing. All threshold shifts were found to be temporary, returning to normal within 24 hours. Normal thresholds: -41 dB at 500 Hz, and -39.7 dB at 800 Hz.

These results can be described as follows: Intense tone stimulation at 800 Hz caused the greatest loss in sensitivity, with higher and lower frequency stimulation tones having a progressively smaller effect. The effect of intense tone stimulation is qualitatively similar for 500 Hz and 800 Hz signals. The frequency of intense tone stimulation was more important in determining the threshold at 800 Hz than the threshold at 500 Hz.

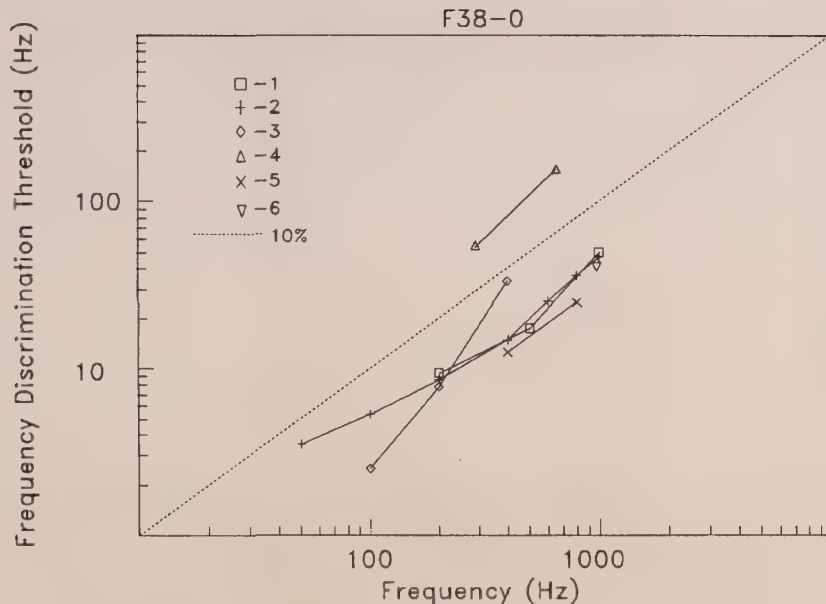


Fig. F38-0. Frequency discrimination thresholds in three otophysan species.

- 1- *Carassius auratus* - goldfish (Jacobs and Tavalga, 1968)
- 2- *Carassius auratus* - goldfish (Fay, 1970)
- 3- *Arius felis* - marine catfish (Tavalga, 1982)
- 4- *Phoxinus laevis* - European minnow (Stetter, 1929)
- 5- *Phoxinus laevis* - European minnow (Dijkgraaf and Verheijen, 1950)
- 6- *Phoxinus laevis* - European minnow (Wohlfahrt, 1939)

References:

- Dijkgraaf, S. and Verheijen, F. (1950) Neue Versuche über das Tonunterscheidungsvermögen der Elritze. *Z. vergl. Physiol.* 32, 248-256.
- Fay, R.R. (1970) Auditory frequency discrimination in the goldfish (*Carassius auratus*). *J. Comp. Physiol. Psychol.* 73, 175-180.
- Jacobs, D.W. and Tavalga, W.N. (1968) Acoustic frequency discrimination in the goldfish. *Anim. Behav.* 16, 67-61.
- Stetter, H. (1929) Untersuchungen über den Gehörsinn der Fische besonders von *Phoxinus laevis* L. und *Amiurus nebulosus* Raf. *Z. vergl. Physiol.* 9, 339-477.
- Tavalga, W.N. (1982) Auditory acuity in the sea catfish (*Arius felis*). *J. Exp. Biol.* 96, 367-376.
- Wohlfahrt, T.A. (1939) Untersuchungen über das Tonunterscheidungsvermögen der Elritze (*Phoxinus laevis* Agass.). *Z. vergl. Physiol.* 26, 570-604.

Table F38-0. Frequency discrimination thresholds in three otophysan species.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)					
	1	2	3	4	5	6
50		3.5				
100		5.3	2.5			
200	9.4	8.6	7.8			
290				55		
400		14.9	33.5		12.5	
500	17.4					
600		25.5				
651				156		
800		36.4			25	
977						41
1000	50.1	46.9				

Notes:

Frequency discrimination in fishes is likely mediated by the central processing of phase-locked peripheral neural activity in the time domain (Fay, 1978). See Piddington (1972) for a demonstration that the goldfish is able to discriminate between acoustic transients which differ only in phase (polarity).

1- Instrumental avoidance conditioning using the staircase psychophysical procedure. Sound levels maintained at 0 dB re: 1 dyne cm⁻² (about 40-45 dB above absolute threshold). Animals trained to detect the change from 1 sec tone pulses of constant frequency to tone pulses alternating between the standard and test frequencies. Means: N=6.

2- Classical respiratory conditioning using the descending method of limits. Sound levels maintained at about 35 dB above absolute detection threshold for 700 msec tone bursts. Means: N=4.

3- Instrumental avoidance conditioning using the method of constant stimuli. Animals trained to detect the change from 1 sec tone pulses of constant frequency to tone pulses alternating between the standard and test frequencies. Thresholds were obtained both for upward and downward frequency changes, and thresholds were considerably smaller for downward transitions at 400 Hz. The average of the "up" and "down" discrimination thresholds are given here. Means: N=10.

4- Conditioned approach for food. Animals were trained in successive discrimination trials to approach for food in the presence of one signal frequency, and not to approach in the presence of another frequency. This conditioning required the animal to retain the "pitch" of the two signals over several minutes. N=1.

5- Conditioned approach for food. Animals trained to detect the change from tone pulses of constant frequency to tone pulses alternating between the standard and test frequencies. Means: N=2.

6- Conditioned approach for food. Animals trained to detect the difference between a "warning" signal (warning that an approach would be punished) of tone bursts alternating in frequency, from a "feeding" signal consisting of tone bursts of constant frequency. This "relative" method was considered to be an improvement over Stetter's (1929) method requiring an "absolute" pitch judgement. The author was unable to demonstrate intensity discrimination in this species with these methods.

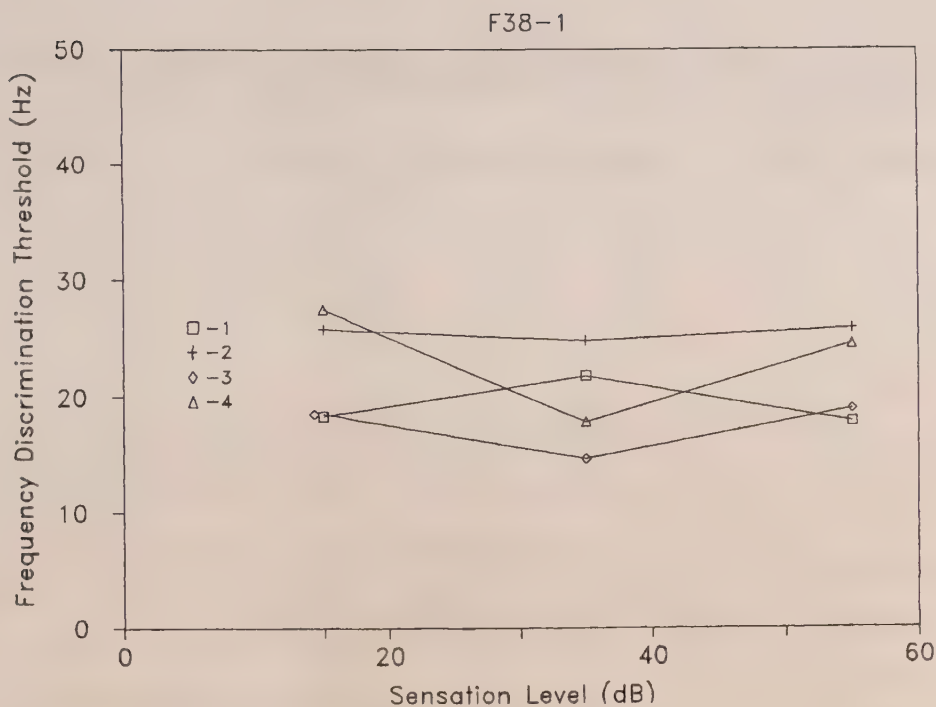


Fig. F38-1. Frequency discrimination in *Carassius auratus* (goldfish) for frequency increments and decrements, and for constant and roving intensity, as a function of sensation level.

- 1- Frequency increment - constant intensity
- 2- Frequency increment - varying intensity
- 3- Frequency decrement - constant intensity
- 4- Frequency decrement - varying intensity

Reference:

Fay, R.R. (1988) Frequency discrimination in the goldfish: Effects of roving intensity, sensation level, and the direction of frequency change. J. Acoust. Soc. Amer. in press.

Table F38-1. Frequency discrimination in *Carassius auratus* (goldfish) for frequency increments and decrements, and for constant and roving intensity, as a function of sensation level.

Sensation Level (dB)	Frequency Discrimination Threshold (Hz)			
	1	2	3	4
15	18.3	25.8	18.5	27.5
35	21.8	24.8	14.6	17.8
55	17.8	25.8	18.9	24.5

Notes:

Classical respiratory conditioning using a tracking psychophysical procedure. Signals were 400 Hz, 500 msec tone bursts with 10 msec rise/fall times, repeated continuously at one per sec. Animals were conditioned to detect the case in which tone burst frequency changed from the repeating standard to a higher or lower value during a seven sec period. Means: N=4.

1- Frequency change was an upward shift in frequency with each tone burst remaining constant in level.

2- Frequency change was an upward shift in frequency with each tone burst randomly varying in level (plus and minus 6 dB range, rectangular distribution).

3- Frequency change was a downward shift in frequency with each tone burst remaining constant in level.

4- Frequency change was a downward shift in frequency with each tone burst randomly varying in level (plus and minus 6 dB range, rectangular distribution).

There are no statistically significant differences among conditions in this experiment. These results show that the frequency discrimination threshold is not likely contaminated by possible loudness difference cues.

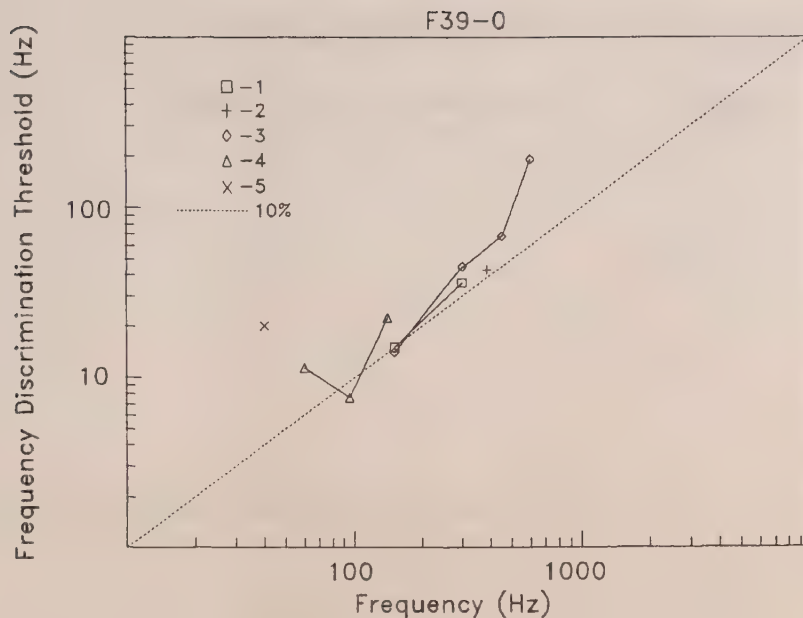


Fig. F39-0. Pure tone frequency discrimination thresholds for five non-otophysan species.

- 1- *Gobius niger* - a goby (Dijkgraaf, 1952)
- 2- *Corvina nigra* - a drum (Dijkgraaf, 1952)
- 3- *Sargus annularis* - ringed sea bream (Dijkgraaf, 1952)
- 4- *Cottus scorpius* - bullhead (Pettersen, 1980 as cited by Enger, 1981)
- 5- *Negaprion brevirostris* - lemon shark (Nelson, 1967)

References:

- Dijkgraaf, S. (1952) Über die Schallwahrnehmung bei Meeresfischen. Z. vergl. Physiol. 34, 104-122.
- Enger, P.S. (1981) Frequency discrimination in teleosts - central or peripheral? In W.N. Tavolga, A.N. Popper and R.R. Fay (eds), Hearing and Sound Communication in Fishes. Springer-Verlag: New York, pp. 243-255.
- Nelson, D.R. (1967) Hearing thresholds, frequency discrimination and acoustic orientation in the lemon shark, *Negaprion brevirostris* (Poey). Bull. Mar. Sci. 17, 741-768.
- Pettersen, L. (1980) Frequency discrimination in the bullhead, *Cottus scorpius*, a fish without swimbladder. Masters Thesis, University of Oslo. Cited in Enger, P.S. (1981) Frequency discrimination in teleosts - central or peripheral? In W.N. Tavolga, A.N. Popper and R.R. Fay (eds), Hearing and Sound Communication in Fishes. Springer-Verlag: New York, pp. 243-255.

Table F39-0. Pure tone frequency discrimination thresholds for five non-otophysan species.

Frequency (Hz)	Just Detectable Change in Frequency (Hz)				
	1	2	3	4	5
40					20
60				11.4	
95				7.6	
140				22.4	
150	15		14		
300	36		45		
385		43			
450			68		
600			192		

Notes:

1-3 Conditioned approach for food. Animals were trained to detect the change from tone pulses of constant frequency to tone pulses alternating between the standard and test frequencies. An attempt was made to present all stimuli at 10-15 dB above absolute detection threshold.

4- Classical cardiac conditioning using the descending method of limits.

5- Classical cardiac conditioning and instrumental shock avoidance (combined thresholds) using descending method of limits. Means: N=2.

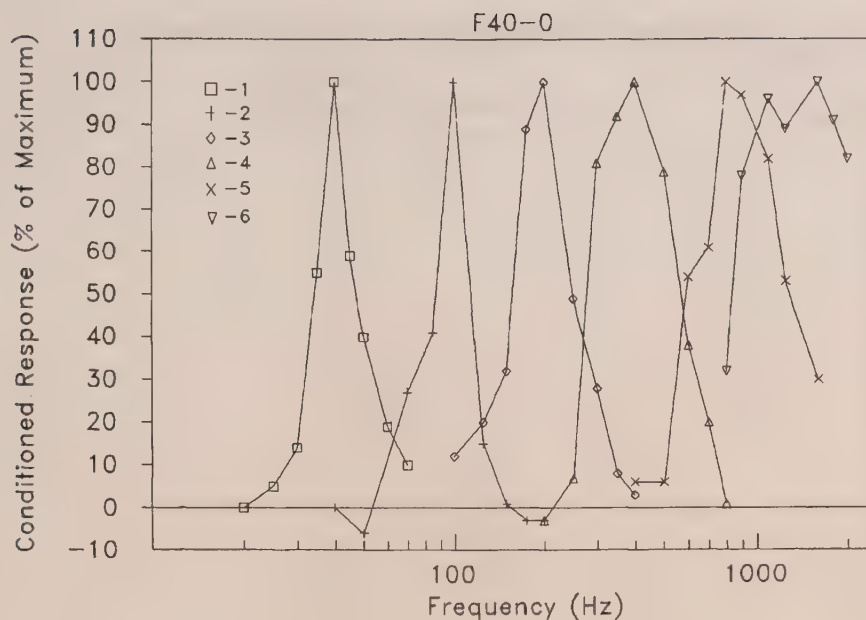


Fig. F40-0. Stimulus generalization gradients for pure tone frequency in *Carassius auratus* (goldfish).

- 1- 40 Hz training frequency
(Fay, 1969a)
- 2- 100 Hz training frequency
- 3- 200 Hz training frequency
- 4- 400 Hz training frequency
- 5- 800 Hz training frequency
- 6- 1600 Hz training frequency
(Fay, 1970a)

References:

- Fay, R.R. (1969a) Auditory sensitivity of the goldfish within the acoustic nearfield. U.S. Naval Submarine Medical Center, Submarine Base, Groton, Connecticut, Report No. 605, 1-11.
- Fay, R.R. (1970a) Auditory frequency generalization in the goldfish (*Carassius auratus*). J. Exp. Anal. Behav. 14, 353-360.

Table F40-0. Stimulus generalization gradients for pure tone frequency in *Carassius auratus* (goldfish).

Frequency (Hz)	Normalized Stimulus Generalization (percent)					
	1	2	3	4	5	6
20	0					
25	5					
30	14					
35	55					
40	100	0				
45	59					
50	40	-6				
60	19					
70	10	27				
85		41				
100		100	12			
125		15	20			
150		1	32			
175		-3	89			
200		-3	100	-3		
250			49	7		
300			28	81		
350			8	92		
400			3	100	6	
500				79	6	
600				38	54	
700				20	61	
800				1	100	32
900					97	78
1100					82	96
1250					53	89
1600					30	100
1800						91
2000						82

Notes:

These results demonstrate that sound frequency is a rather simple monotonic perceptual dimension for the goldfish, similar to the perceptual dimension of pure tone pitch for humans. Compare these data with those for a bird (Fig. B35-0).

Classical respiratory conditioning consists of the presentation of a conditioned stimulus for about 6 sec, followed by a brief electric shock across the animal's body. The shock causes a brief respiratory suppression, and after 5 to 10 conditioning trials, the conditioned stimulus elicits suppression. Animals were trained to respond to a single pure tone (training frequency), and then tested four times, without reinforcement, to each of several neighboring tone frequencies at 30 dB SL. Data are medians of responses pooled across four animals.

The normalized stimulus generalization was calculated such that the degree of respiratory suppression elicited by the training frequency stimulus was defined as 100%, and the response measure expected by chance was defined as 0%. Generalization below 0% indicates an acceleration of respiration.

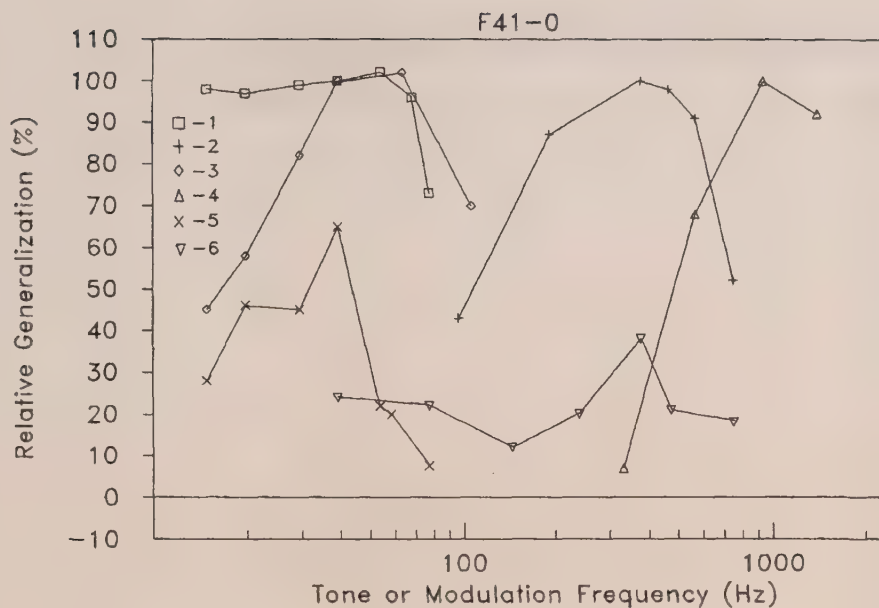


Fig. F41-0. Generalization gradients along various dimensions of sinusoidally amplitude modulated signals in *Carassius auratus* (goldfish).

Training	Test
1- 400 Hz modulated at 40 Hz.	Vary modulation frequency
2- 400 Hz modulated at 40 Hz	Vary carrier frequency
3- 1000 Hz modulated at 40 Hz	Vary modulation frequency
4- 1000 Hz modulated at 40 Hz	Vary carrier frequency
5- 40 Hz pure tone	Vary modulation frequency of 1000 Hz carrier
6- 400 Hz modulated at 40 Hz	Vary pure tone frequency

Reference:

Fay, R.R. (1972) Perception of amplitude-modulated auditory signals by the goldfish.
J. Acoust. Soc. Amer. 52, 660-666.

Table F41-0. Generalization gradients along various dimensions of sinusoidally amplitude modulated signals in *Carassius auratus* (goldfish).

Frequency (Hz)	Normalized Stimulus Generalization (percent)					
	1	2	3	4	5	6
15	98		45		28	
20	97		58		46	
30	99		82		45	
40	100		100		65	24
55	102				22	
60					20	
65			102			
70	96					
80	73				7.5	22
100		43				
110			70			
150						12
200		87				
250						20
350				7		
400		100				38
490		98				
500						21
600		91		68		
800		52				18
1000				100		
1500				92		

Notes:

The stimulus generalization paradigm is used here to ask which dimensions of a complex amplitude-modulated sound come to control a behavioral response. In general, training with amplitude modulated tones leads to decrements in generalization for changes in both the carrier and modulation frequency. Curve #5 shows that there is a perceptual similarity between a 40 Hz pure tone (training stimulus) and a 1000 Hz tone modulated at 40 Hz. This is a demonstration of periodicity pitch in the goldfish.

Classical respiratory conditioning. Modulated signals presented at 100% modulation. All signals were presented 30 dB SL. Four animals per group. Data are medians of four response measures per test condition per fish.

See Notes for Fig. F40-0.

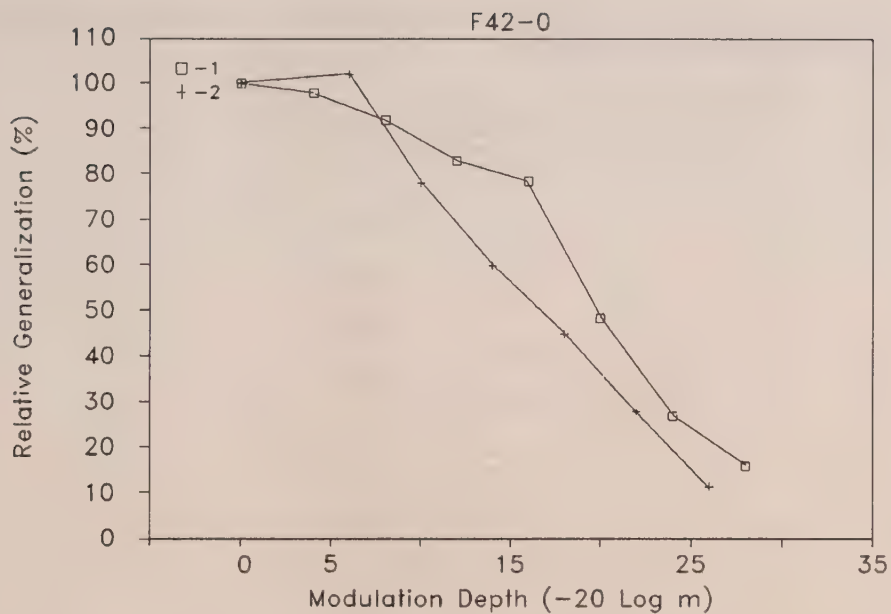


Fig. F42-0. Generalization gradients for modulation depth for amplitude modulated sinusoids in *Carassius auratus* (goldfish).

- 1- 1000 Hz carrier modulated at 40 Hz
- 2- 400 Hz carrier modulated at 40 Hz

Reference:

Fay, R.R. (1972) Perception of amplitude-modulated auditory signals by the goldfish. J. Acoust. Soc. Amer. 52, 660-666.

Table F42-0. Generalization gradients for modulation depth for amplitude modulated sinusoids in *Carassius auratus* (goldfish).

Modulation Depth (-20 Log m)	Normalized Stimulus Generalization (percent)	
	1	2
0	100	100
4	98	
6		102
8	92	
10		78
12	83	
14		60
16	78.5	
18		45
20	48.5	
22		28
24	27	
26		11.5
28	16	

Notes:

All signals presented 30 dB SL.

See Notes for Figs. F44-0 for definition of -20 Log m. See notes for Fig. F40-0 for definition of Normalized Stimulus Generalization.

Classical respiratory conditioning. All signals were presented 30 dB SL. Four animals per group. Data are medians of four response measures per test condition per fish.

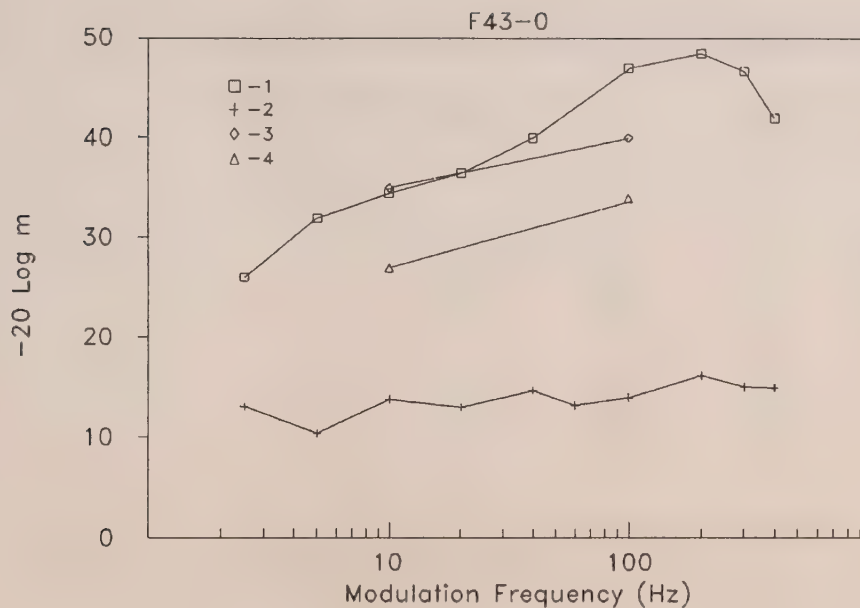


Fig. F43-0. Temporal modulation transfer function for tones and noise in *Carassius auratus* (goldfish).

- 1- 800 Hz tone (Fay, 1980)
- 2- Broad band noise (Fay, 1980)
- 3- 800 Hz tone (Coombs and Fay, 1985)
- 4- 200 Hz tone (Coombs and Fay, 1985)

References:

- Coombs, S. & Fay, R. R. (1985) Adaptation effects on amplitude modulation detection: behavioral and neurophysiological assessment in the goldfish auditory system. *Hear. Res.* 19, 57-71.
- Fay, R.R. (1980) Psychophysics and neurophysiology of temporal factors in hearing by the goldfish: Amplitude modulation detection. *J. Neurophysiol.* 44, 312-332.

Table F43-0. Temporal modulation transfer function for tones and noise in *Carassius auratus* (goldfish).

Modulation Frequency (Hz)	Minimum Detectable Modulation Depth (-20 Log m)			
	1	2	3	4
2.5	26	13		
5	32	10.4		
10	34.5	13.8	35	27
20	36.5	13		
40	40	14.7		
60		13.2		
100	47	14	40	34
200	48.5	16.2		
300	46.7	15.1		
400	42	15		

Notes:

The temporal modulation transfer function (TMTF) describes how the minimum detectable depth of sinusoidal amplitude modulation (SAM) varies as a function of modulation frequency. The TMTF provides a systematic description of how the auditory system detects temporal envelope patterns, and can be thought of as the frequency response function of an envelope detector. The waveform carrier that is amplitude-modulated is usually noise, since the process of modulation produces no changes in the long-term amplitude spectrum of the noise carrier signal. Thus, detection of SAM on a noise carrier is not mediated by a spectral cue. With pure tone carrier signals, however, modulation produces spectral energy at frequencies equal to the carrier frequency plus the modulation frequency, and the carrier minus the modulation frequency. Thus for pure tones, there is a spectral "solution" to the modulation detection problem. In this case, the interesting question is whether a given system uses temporal or spectral information to solve the problem.

The degree of amplitude modulation is measured as the index of modulation (m). The value m is equal to $(P-T)/(P+T)$, where P is the sound pressure at an envelope maximum, and T is the pressure at an envelope trough, or minimum.

1- Classical respiratory conditioning using the descending method of limits.

Carrier signal was a continuous 800 Hz tone at 35 dB sensation level (SL). Means: N=4.

2- Same as 1 except that the carrier was noise.

3- Same as 1 except that carrier was an 800 Hz pure tone at 30 dB SL.

4- Same as 3 except that carrier was 200 Hz pure tone.

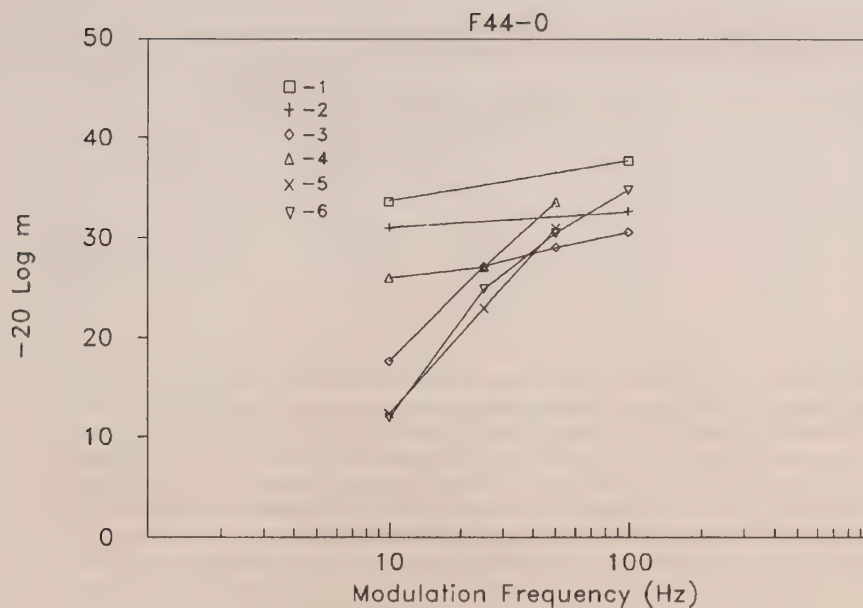


Fig. F44-0. Portions of the temporal modulation transfer function for tones under various conditions in *Carassius auratus* (goldfish).

- 1- 800 Hz carrier continuous; modulation continuous
- 2- 800 Hz carrier continuous; modulation in 500 msec bursts
- 3- 800 Hz carrier 500 msec bursts; modulation in 500 msec bursts
- 4- 200 Hz carrier continuous; modulation continuous
- 5- 200 Hz carrier 500 msec bursts; modulation in 500 msec bursts
- 6- 570 Hz carrier 500 msec bursts; modulation in 500 msec bursts

Reference:

Coombs, S. and Fay, R.R. (1985) Adaptation effects on amplitude modulation detection: behavioral and neurophysiological assessment in the goldfish auditory system. *Hear. Res.* 19, 57-71.

Table F44-0. Portions of the temporal modulation transfer function for tones under various conditions in *Carassius auratus* (goldfish).

Modulation Frequency (Hz)	Minimum Detectable Modulation Depth (-20 Log m)					
	1	2	3	4	5	6
10	33.6	31	17.7	26	12.4	12
25			27.2	27.1	23	24.9
50			29.1	33.6	31	30.5
100	37.7	32.7	30.6			34.8

Notes:

See notes for Fig. F43-0. The rationale for this series of experiments was to investigate the effect of long term adaptation (continuous versus pulsed carrier), the onset of modulation (continuous versus pulsed modulation), and the effect of carrier frequency on the detectability of modulation. In addition, conditions were run using a pulsed 800 Hz carrier in which the overall intensity of each burst was drawn at random from a rectangular distribution having a range of 20 dB. This intensity fluctuation had no effect on measured modulation detection thresholds. Classical respiratory conditioning using the staircase psychophysical procedure. Carrier signals were either 200, 570 or 800 Hz pure tones at 35 dB sensation level (SL). Means: N=4.

1- The stimulus condition here was similar to that used in Fig. F43-0. The carrier tone was presented continuously, and the modulation (conditioned stimulus) was continuous SAM added to the carrier for 7 sec.

2- Same as #1 except that the modulation was pulsed on and off (500 msec on, 500 msec off).

3- Same as #1 except that the carrier was presented pulsed (500 msec on and 500 msec off), and the conditioned stimulus consisted of the substitution of SAM tone bursts for unmodulated tone bursts.

4- Same as 1 except that carrier was 200 Hz pure tone.

5- Same as 3 except that carrier was 200 Hz pure tone.

6- Same as 3 except that carrier was 570 Hz pure tone.

Note that pulsing the modulation or pulsing the entire signal results in poor modulation detection sensitivity at low modulation frequencies.

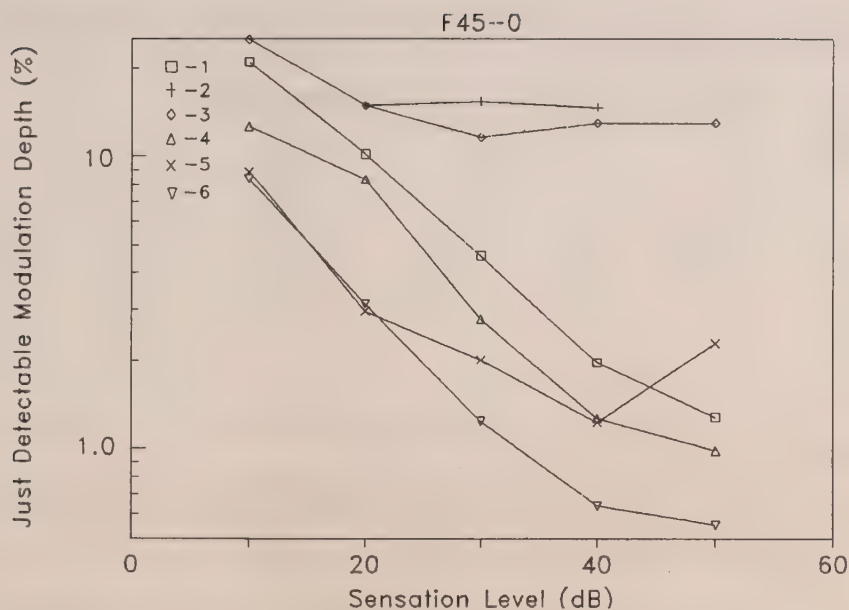


Fig. F45-0. The effect of sound pressure level on amplitude modulation detection in *Carassius auratus* (goldfish).

- 1- 2.5 Hz modulation; 800 Hz carrier continuous (Fay, 1980)
- 2- 2.5 Hz modulation; noise carrier continuous (Fay, 1980)
- 3- 10 Hz modulation; 800 Hz carrier pulsed (Coombs and Fay, 1985)
- 4- 100 Hz modulation; 800 Hz carrier pulsed (Coombs and Fay, 1985)
- 5- 10 Hz modulation; 800 Hz carrier continuous (Coombs and Fay, 1985)
- 6- 100 Hz modulation; 800 Hz carrier continuous (Coombs and Fay, 1985)

References:

- Coombs, S. & Fay, R.R. (1985) Adaptation effects on amplitude modulation detection: behavioral and neurophysiological assessment in the goldfish auditory system. *Hear. Res.* 19, 57-71.
- Fay, R.R. (1980) Psychophysics and neurophysiology of temporal factors in hearing by the goldfish: Amplitude modulation detection, *J. Neurophysiol.* 44, 312-332.

Table F45-0. The effect of sound pressure level on amplitude modulation detection in *Carassius auratus* (goldfish).

Sensation Level (dB)	Minimum Detectable Modulation Depth (Percent)					
	1	2	3	4	5	6
10	20.9		25	12.6	8.9	8.4
20	10.2	14.9	14.9	8.4	2.98	3.16
30	4.6	15.4	11.6	2.8	2.04	1.26
40	2	14.7	13	1.29	1.25	0.65
50	1.3		13	1	2.32	0.56

Notes:

See Notes for Fig. F43-0. Classical respiratory conditioning using the staircase psychophysical procedure. Means: N=4.

1- The stimulus condition here was similar to that used in Fig. F43-0. The carrier tone was presented continuously, and the modulation (conditioned stimulus) was continuous SAM added to the carrier for 7 sec.

2- Same as #1 except that the modulation was pulsed on and off (500 msec on, 500 msec off).

3- Same as #1 except that the carrier was presented pulsed (500 msec on and 500 msec off), and the conditioned stimulus consisted of the substitution of SAM tone bursts for unmodulated tone bursts.

4- Same as #1 except that carrier was 200 Hz pure tone.

5- Same as #3 except that carrier was 200 Hz pure tone.

6- Same as #3 except that carrier was 570 Hz pure tone.

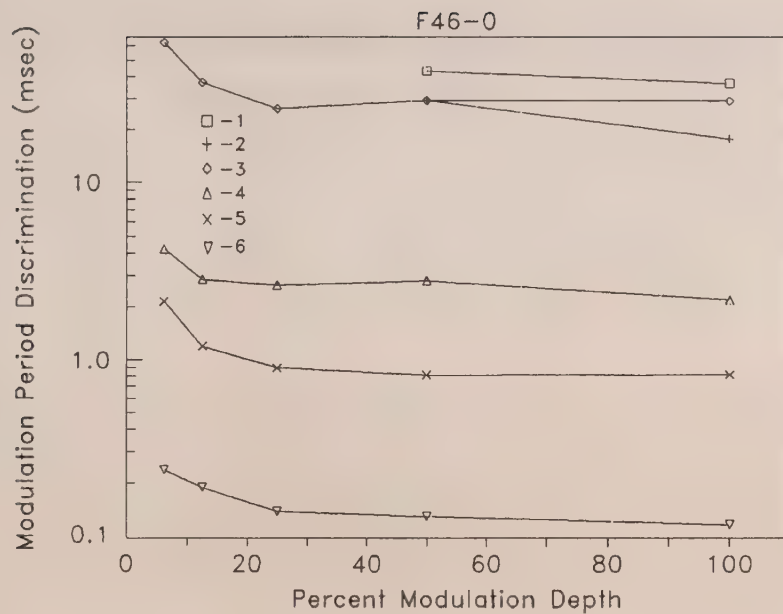


Fig. F46-0. The effect of amplitude modulation depth on modulation period discrimination in *Carassius auratus* (goldfish).

- 1- Broad band noise carrier; 20 Hz modulation rate
- 2- Broad band noise carrier; 50 Hz modulation rate
- 3- 800 Hz tone carrier; 20 Hz modulation rate
- 4- 800 Hz 50 Hz
- 5- 800 Hz 100 Hz
- 6- 800 Hz 200 Hz

Reference:

Fay R.R. (1982) Neural mechanisms of an auditory temporal discrimination by the goldfish. J. Comp. Physiol. 147, 201-216.

Table F46-0. The effect of amplitude modulation depth on modulation period discrimination in *Carassius auratus* (goldfish).

Modulation Depth (%)	Modulation Period Discrimination (msec)					
	1	2	3	4	5	6
6.25			59	4.1	2.1	0.238
12.5			35	2.78	1.18	0.19
25			25	2.6	0.89	0.14
50	41	28	28	2.75	0.81	0.132
100	35	17	28	2.15	0.82	0.119

Notes:

In these experiments, animals were trained to detect the condition in which the modulation rate (in Hz) of an amplitude modulated sound changed from a steady rate to a sinusoidally (2.5 Hz) varying rate. The task is essentially discriminating a steady modulation rate from a changing one. The smallest detectable change in rate (peak-peak sinusoidal frequency modulation, in Hz) was measured and then recalculated as the smallest detectable change in period (in msec). All signals were presented 35 dB SL (sensation level, or level above threshold). This experiment essentially asks how the just-detectable change in modulation period depends on the depth of amplitude modulation at different modulation rates.

Classical respiratory conditioning using the descending method of limits. Means: N=4.

Comparisons with neurophysiological data obtained on goldfish auditory (saccular) nerve fibers under the same stimulus conditions showed that the discrimination significantly deteriorated at modulation depths leading to a modulation period synchronization coefficient of 0.5 or below.

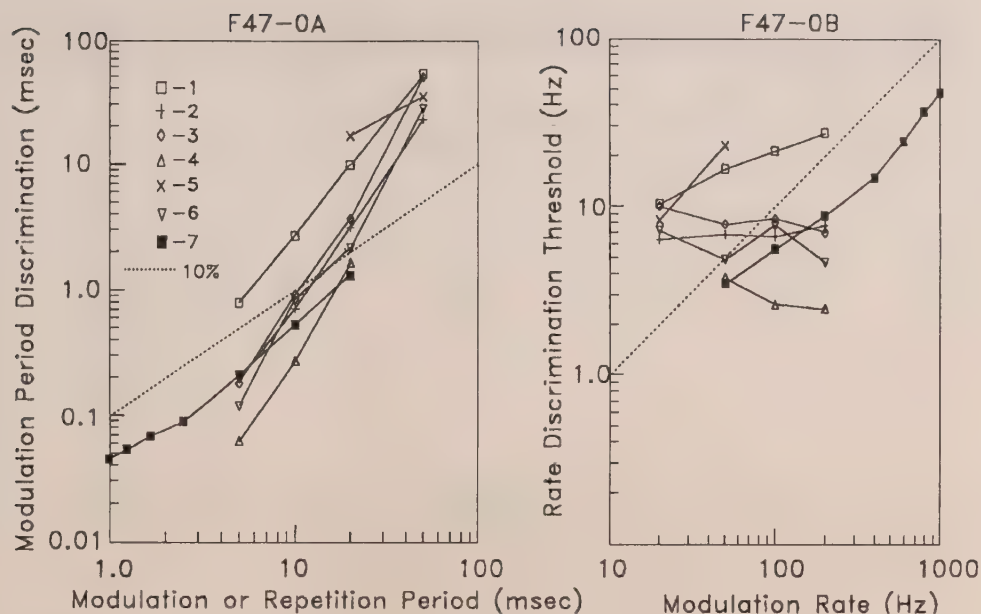


Fig. F47-0. A. Modulation period (or repetition period) discrimination thresholds as a function of repetition period for a variety of different periodic signals in *Carassius auratus* (goldfish). B. Modulation rate discrimination thresholds as a function of modulation rate.

- 1- Gaussian noise bursts; 2.5 Hz rate modulation (Fay and Passow, 1982)
- 2- "FM" noise bursts; 2.5 Hz rate modulation (Fay and Passow, 1982)
- 3- Filtered clicks; 2.5 Hz rate modulation (Fay and Passow, 1982)
- 4- Filtered clicks; random rate modulation (Fay and Passow, 1982)
- 5- SAM noise; 2.5 Hz rate modulation (Fay, 1982)
- 6- SAM 800 Hz tone; 2.5 Hz rate modulation (Fay, 1982)
- 7- Pure tone frequency discrimination (Fay, 1970a)

References:

- Fay, R.R. (1970a) Auditory frequency discrimination in the goldfish (*Carassius auratus*). J. Comp. Physiol. Psychol. 73, 175-180.
- Fay, R.R. (1982) Neural mechanisms of an auditory temporal discrimination by the goldfish. J. Comp. Physiol. 147, 201-216.
- Fay, R.R. and Passow, B. (1982) Temporal discrimination in the goldfish. J. Acoust. Soc. Amer. 72, 753-760.

Table F47-0A. Modulation period (or repetition period) discrimination thresholds as a function of repetition period for a variety of different periodic signals in *Carassius auratus* (goldfish).

Repetition Period (msec)	Repetition Period Discrimination (msec)						
	1	2	3	4	5	6	7
50	53	23	50		35	28	
20	10	3.15	3.7	1.65	17	2.15	1.31
10	2.7	0.71	0.92	0.27		0.82	0.53
5	0.7	0.2	0.18	0.063		0.119	0.21
2.5							0.089
1.67							0.068
1.25							0.054
1.0							0.045

Notes:

These experiments investigate how the threshold for detecting a change in the period of a periodic envelope or waveform depends on the envelope shape, carrier signal, and repetition rate. Classical respiratory conditioning using the descending method of limits. All signals presented 35 dB SL. Means: N=4.

1- "Gaussian noise bursts" were produced by gating on noise (band pass filtered from 1 to 1.6 kHz) for 2.5 msec with 2.5 msec rise/fall times.

2- "FM noise bursts" were produced by gating on a noise signal for 2.5 msec with 2.5 msec rise/fall times. The noise signal was produced by frequency modulating a 1 kHz tone using a noise waveform (low-pass filtered at 160 Hz). This produced a noise with a smaller amplitude variation than #1 above.

3- "Filtered clicks" were produced by passing one cycle of an 800 Hz tone (gated on and off at zero-crossings) through a 1 to 1.6 kHz band pass filter.

4- Same signals as in #3 above except that the variation in click repetition rate (conditioned stimulus) was produced by randomly modulating repetition rate, rather than sinusoidally modulating the rate. The random modulating signal was 1.6 kHz low-pass noise. Threshold defined as RMS variation in inter-click-interval.

5- Same data as in Fig. F46-0, #1 and #2, 100% SAM broad band noise.

6- Same data as in Fig. F46-0, #3-6, 100% SAM 800 Hz pure tone.

7- Same data as in F38-0 (#2), transformed from a frequency discrimination threshold to a period discrimination threshold. Thresholds are similar for frequency and envelope discrimination, but the former function has a lower slope.

Table F47-0B. Modulation rate discrimination thresholds as a function of modulation rate.

Modulation Rate (Hz)	Modulation Rate Discrimination Threshold (Hz)					
	1	2	3	4	5	6
20	10.3	6.3	10		8.2	7.2
50	16.7	6.8	7.8	3.8	22.9	4.9
100	21.3	6.6	8.4	2.6		7.6
200	27.3	7.7	6.9	2.5		4.6

Notes:

Same data as in Fig. F47-0A calculated as rate discrimination thresholds. Tone frequency discrimination data, replotted for comparison here, are in Table F38-0.

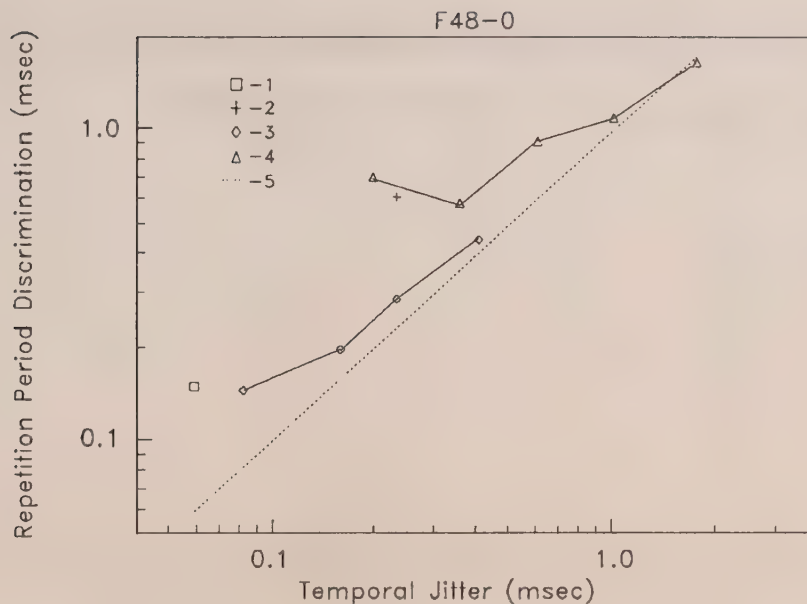


Fig. F48-0. The effect of random inter-burst-interval jitter on the detection of a slow change of inter-burst-interval of filtered clicks in *Carassius auratus* (goldfish).

- 1- 200 Hz repetition rate; 0 msec stimulus jitter
- 2- 100 Hz repetition rate; 0 msec stimulus jitter
- 3- 200 Hz repetition rate; stimulus jitter manipulated
- 4- 100 Hz repetition rate; stimulus jitter manipulated
- 5- Points at which the modulation period discrimination threshold (in msec) would equal the random jitter imposed on the otherwise periodic inter-burst-interval.

Reference:

Fay, R.R. and Passow, B. (1982) Temporal discrimination in the goldfish. *J. Acoust. Soc. Amer.* 72, 753-760.

Table F48-0. The effect of random inter-burst-interval jitter on the detection of a slow change of inter-burst-interval of filtered clicks in *Carassius auratus* (goldfish).

RMS Inter-burst-interval jitter (msec)	Repetition Period Discrimination (msec)			
	1	2	3	4
0.06	0.16			
0.085			0.155	
0.17			0.215	
0.215				0.83
0.255		0.71	0.32	
0.4				0.68
0.46			0.51	
0.7				1.1
1.2				1.32
2.15				2.05

Notes:

This experiment asks how a "background" of random jitter in an otherwise periodic train of filtered clicks affects the animal's ability to detect a slow change (2.5 Hz sinusoidal) in repetition period. The results show, among other things, that at large degrees of jitter in the stimulus, the repetition period discrimination threshold approaches the stimulus jitter (the standard deviation of inter-burst-interval). These data estimate the "internal" jitter which presumably limits normal inter-burst-interval discrimination (#1 and 2).

Classical respiratory conditioning using the descending method of limits. Means: N=4.

1- This point locates 2 independent thresholds. The just detectable amount of random jitter for filtered clicks repeated at 200 Hz is plotted on the abscissa (from #3, Fig. F47-0). The just detectable change in 2.5 Hz sinusoidal jitter at 200 Hz is plotted on the ordinate (from #4, Fig. F47-0).

2- This point locates 2 independent thresholds. The just detectable amount of random jitter for filtered clicks repeated at 100 Hz is plotted on the abscissa (from #3, Fig. F47-0). The just detectable change in 2.5 Hz sinusoidal jitter at 100 Hz is plotted on the ordinate (from #4, Fig. F47-0).

3- With a base repetition rate of 200 Hz, repetition period discrimination thresholds are shown as a function of the amount of random jitter imposed on the otherwise periodic inter-burst-interval. Random jitter added by frequency-modulating the periodic signal controlling burst repetition rate with a low pass (1.6 kHz) noise waveform.

4- With a base repetition rate of 100 Hz, repetition period discrimination thresholds are shown as a function of the amount of random jitter imposed on the otherwise periodic inter-burst-interval. Random jitter added by frequency-modulating the periodic signal controlling burst repetition rate with a low pass (1.6 kHz) noise waveform.

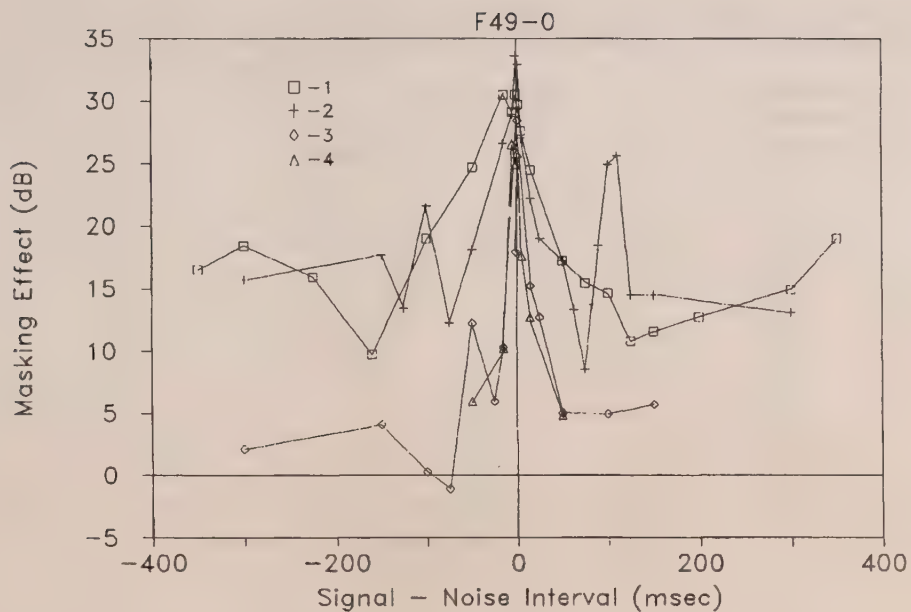


Fig. F49-0. Non-simultaneous masking of tones by noise in *Carassius auratus* (goldfish).

1- 15 msec signal: 250 msec noise masker
 2- 25 msec 250 msec
 3- 50 msec 250 msec
 4- 15 msec 50 msec

Reference:

Popper, A.N. and Clarke, N.L. (1979) Non-simultaneous auditory masking in the goldfish *Carassius auratus*. J. Exp. Biol. 83, 145-158.

Table F49-0. Non-simultaneous masking of tones by noise in *Carassius auratus* (goldfish).

Inter-Stimulus Interval (msec)	Masking Effect (dB)			
	1	2	3	4
-350	16.5			
-300	18.4	15.7	2.1	
-225	15.9			
-160	9.7			
-150		17.7	4.1	
-125		13.4		
-100	19	21.6	0.3	
-75		12.3	-1.1	
-50	24.7	18.1	12.2	5.9
-25			5.9	
-15	30.5	26.6	10.3	10.2
-5	29.1	28.9		26.5
-1	30.5	33.6	17.9	24.9
1	29.7	32.9	28.4	25.8
5	27.6	27		17.6
15	24.5	22.2	15.2	12.7
25		19	12.7	
50	17.2	17.2	5	4.8
63		13.3		
75	15.4	8.5		
83		13.7		
90		18.4		
100	14.6	24.9	4.9	
110		25.6		
125	10.8	14.5		
150	11.6	14.5	5.7	
200	12.7			
300	14.9	13.1		
350	19			

Notes:

The negative time values indicate the case in which the signal preceeded the masker in time (backward masking). The time in this case is the interval between the end of the signal and the beginning of the masker. The positive time values indicate the opposite case (forward masking), where the time is the interval between masker offset and signal onset.

The masker was noise bursts, bandpass filtered at 500 Hz, presented periodically once per second for the indicated duration. Signal was a 500 Hz tone. The masking effect is the decibel difference between the threshold for the signal in quiet and the threshold in the presence of the masker. Note that there is a masking effect which extends over 300 msec prior to and following the masker. This temporally remote masking may be due to a long term adaptation effect caused by the constantly repeating masker.

Classical respiratory conditioning using the staircase psychophysical procedure. Means: N=4.

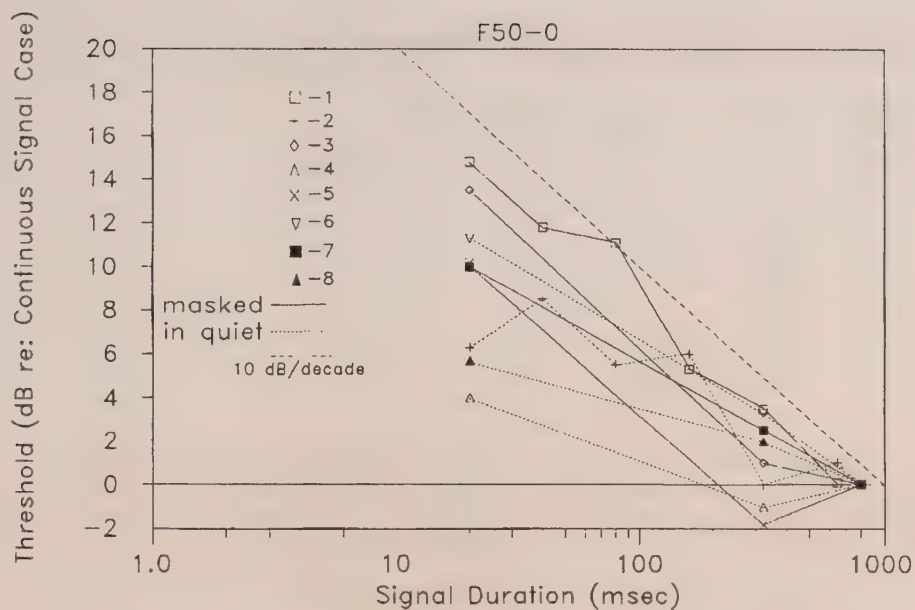


Fig. F50-0. Quiet and masked pure tone thresholds as a function of signal duration in *Carassius auratus* (goldfish).

- 1- 400 Hz, -25 dB noise spectrum level
- 2- 400 Hz, in quiet
- 3- 800 Hz, -25 dB noise spectrum level
- 4- 800 Hz, in quiet
- 5- 200 Hz, -25 dB noise spectrum level
- 6- 200 Hz, in quiet
- 7- Noise, -25 dB noise spectrum level
- 8- Noise, in quiet

References:

- Fay, R.R. and Coombs, S. (1983) Neural mechanisms in sound detection and temporal summation. *Hear. Res.* 10, 69-92.

Table F50-0. Quiet and masked pure tone thresholds as a function of signal duration in *Carassius auratus* (goldfish).

Signal Duration (msec)	Signal Threshold (dB re: threshold for continuous tone)							
	1	2	3	4	5	6	7	8
20	14.8	6.3	13.5	4	10.2	11.3	10	5.7
40	11.8	8.5						
80	11.1	5.5						
160	5.3	6						
320	3.5	0	1	-1	-1.8	3.3	2.5	2
640	0.1	1						
cont.	0	0	0	0	0	0	0	0

Notes:

Classical respiratory conditioning using the staircase psychophysical procedure. Means: N=4. "Cont." indicates the condition in which the signal was "on" continuously during the seven sec conditioned stimulus interval. In all other conditions, signals of the indicated duration were pulsed once per sec during the conditioned stimulus interval.

1- Least squares linear best fit to signal threshold in dB and log duration has a slope (power function exponent) of -1.04.

2- Slope of -0.43 (quiet)

3- Slope of -0.94 (masked)

4- Slope of -0.42 (quiet)

5- Slope of -1.01 (masked)

6- Slope of -0.51 (quiet)

7- Slope of -0.67 (masked)

8- Slope of -0.34 (quiet)

In general, these data show that sound intensity summates nearly linearly for the case in which tones are detected in a noise background, but summate less efficiently in quiet. The difference may be due to greater neural adaptation in quiet. In general, the slopes of these functions are lower for noise signals than for tone signals.

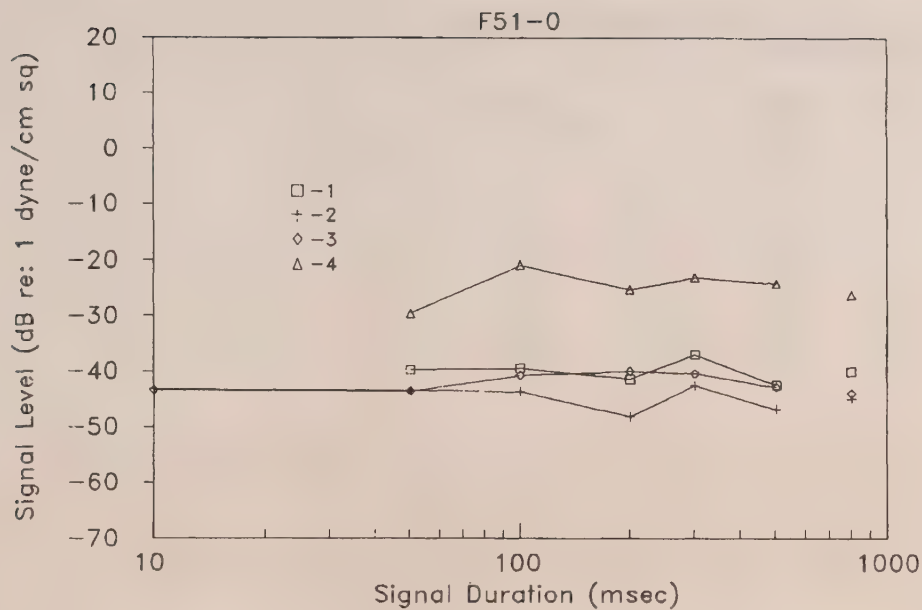


Fig. F51-0. Quiet thresholds for tones as a function of signal duration in *Carassius auratus* (goldfish).

- 1- 300 Hz
- 2- 500 Hz
- 3- 1000 Hz
- 4- 1500 Hz

Reference:

Popper, A.N. (1972) Auditory threshold in the goldfish (*Carassius auratus*) as a function of signal duration. J. Acoust. Soc. Amer. 52, 596-602.

Table F51-0. Quiet thresholds for tones as a function of signal duration in *Carassius auratus* (goldfish).

Signal Duration (msec)	Threshold (dB re: 1 dyne cm ⁻²)			
	1	2	3	4
10		-43.2	-43.4	
50	-39.7	-43.4	-43.5	-29.5
100	-39.4	-43.6	-40.7	-20.8
200	-41.4	-48.1	-40	-25.2
300	-37	-42.6	-40.4	-23
500	-42.5	-46.8	-42.8	-24.1
Cont.	-40.1	-44.9	-43.9	-26.1

Notes:

Instrumental avoidance conditioning using the staircase psychophysical procedure. Means: N=4. "Cont." refers to the condition in which the signal was presented continuously during the conditioned stimulus interval.

The table below shows the duty cycle associated with each signal duration used in this experiment.

On time (msec)	Off Time (msec)	Percent of Time Signal is On
10	490	2
50	500	9.1
100	500	16.7
200	500	28.6
300	700	30
500	500	50

These data, and data from the same study in Fig. F54-0 show no effects of signal duration on sound detection. Data from two other studies on the goldfish (Figs. F50-0, F52-2, and one study on the cod (Fig. F53-0) show that in general, thresholds decline for longer duration signals. The present study was carried out in quiet while those of Figs. F52-0 and F53-0 were carried out with a noise background. The data in Fig F50-0 show that the degree of temporal summation declines in quiet conditions relative to masked conditions.

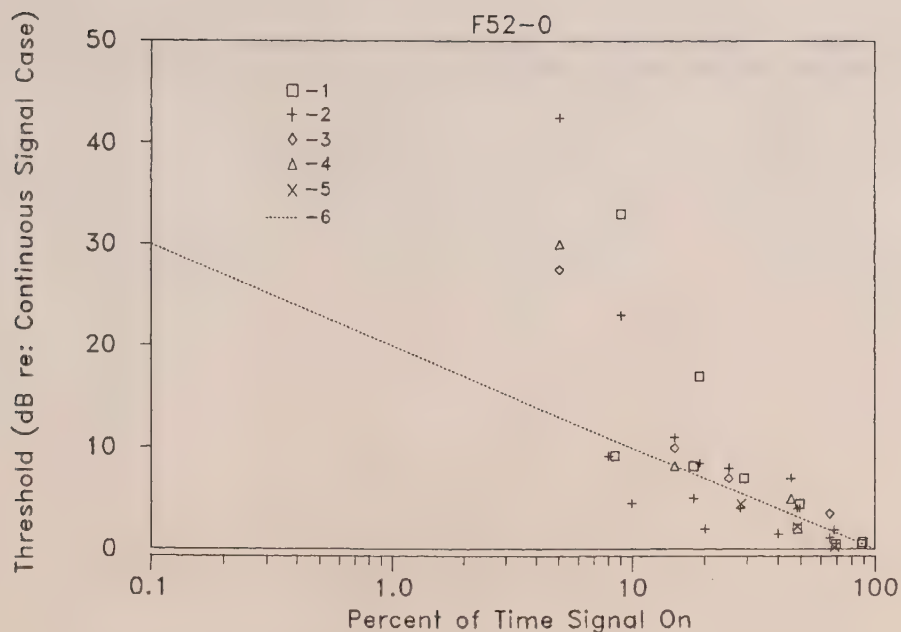


Fig. F52-0. The effect of duty cycle (percent time signal is on) on pure tone thresholds in *Carassius auratus* (goldfish).

- 1- 500 msec pulse period, 400 Hz
- 2- 250 msec, 400 Hz
- 3- 100 msec, 400 Hz
- 4- 50 msec, 400 Hz
- 5- 250 msec, 1500 Hz
- 6- Perfect time-intensity trading for equal energy at threshold (10 dB/decade of duty cycle)

Reference:

Offutt, G.C. (1967) Integration of the energy in repeated tone pulses by man and the goldfish. *J. Acoust. Soc. Amer.* 41, 13-19.

Table F52-0. The effect of duty cycle (percent time signal is on) on pure tone thresholds in *Carassius auratus* (goldfish).

Percent Time Signal On	Threshold (dB re: continuous threshold)				
	1	2	3	4	5
5			27.5	30	
8		42.5			
8.5	9.2	9.2			
9	33				
10		23			
15		4.5	10	8.2	
18	8.2	11			
19	17	5			
20		8.5			
25		2	7		
28		8			4.5
29	7	4			
45		1.5		5	
48	2	7			2.2
49	4.5	4			
60		4			
65			3.5		
68		1.1			0.2
69	0.5	1.9			
88	0.5	0.5			
89	0.7				

Notes:

Classical cardiac conditioning using the method of limits. Data are medians of thresholds for 2 animals for conditions #1 and 2, and for one animal for conditions #3,4, and 5. Rise/fall times 5 msec for conditions #1, 2, 3, and 5; 2.5 msec for #4. Some thresholds of condition #2 were determined with 25 msec rise/fall times. These are not different from the thresholds determined using 5 msec rise/fall times.

Pulse period refers to the reciprocal of the repetition rate of sound pulses to be detected.

Although the conditions of the experiment are nominally in quiet, a high noise level produced by the electronic switch probably resulted in these thresholds being masked.

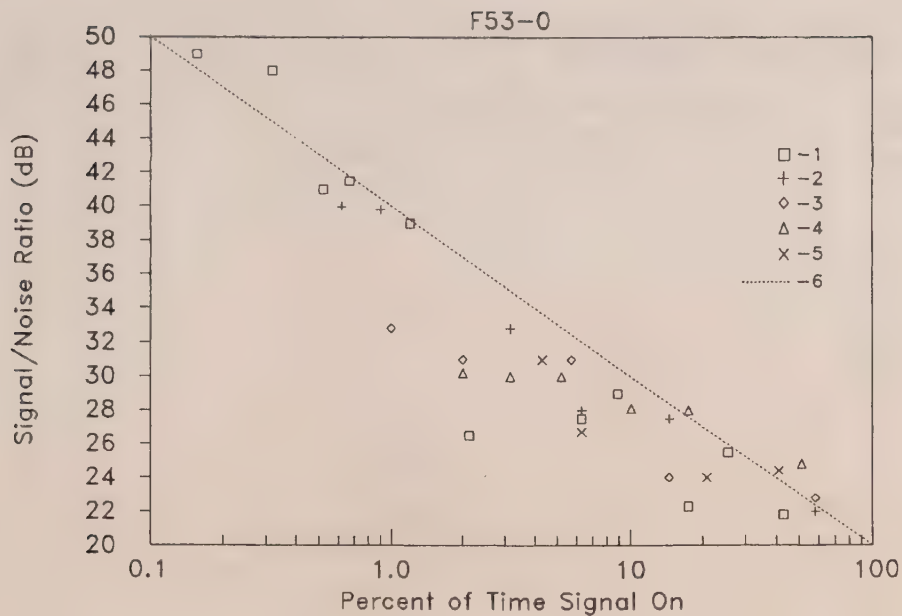


Fig. F53-0. The effect of duty cycle (percent time stimulus on) on pure tone thresholds in *Gadus morhua* (cod).

- 1- 8-25 msec signal duration
- 2- 30-40 msec
- 3- 50-60 msec
- 4- 100 msec
- 5- 210 msec
- 6- Perfect time-intensity trading for equal energy at threshold (10 dB/decade of duty cycle)

Reference:

Hawkins, A.D. (1981) The hearing abilities of fish. In W.N. Tavolga, A.N. Popper and R.R. Fay (eds), *Hearing and Sound Communication in Fishes*. Springer-Verlag: New York, pp. 109-137.

Table F53-0. The effect of duty cycle (percent time stimulus on) on pure tone thresholds in *Gadus morhua* (cod).

Percent Time Signal On	Signal-To-Noise Ratio at Threshold (dB)				
	1	2	3	4	5
0.156	49				
0.32	48				
0.52	41				
0.62		40			
0.67	41.5				
0.9		39.8			
1			32.8		
1.2	39				
2			31	30.2	
2.13	26.5				
3.16		32.8		30	
4.3					31
5.2				30	
5.7			31		
6.3	27.5	28			26.7
8.9	29				
10.1				28.1	
14.5		27.5	24		
17.4	22.3			28	
20.8					24
25.4	25.5				
41					24.4
42.6	21.8				
51				24.8	
58		22	22.8		

Notes:

These data are reported in a book chapter as by Hawkins and Horner but no detailed reference was given. Although few experimental details were given, signals were apparently masked by broad band noise. It is expected that the experimental methods are similar to those in other experimental papers by Hawkins.

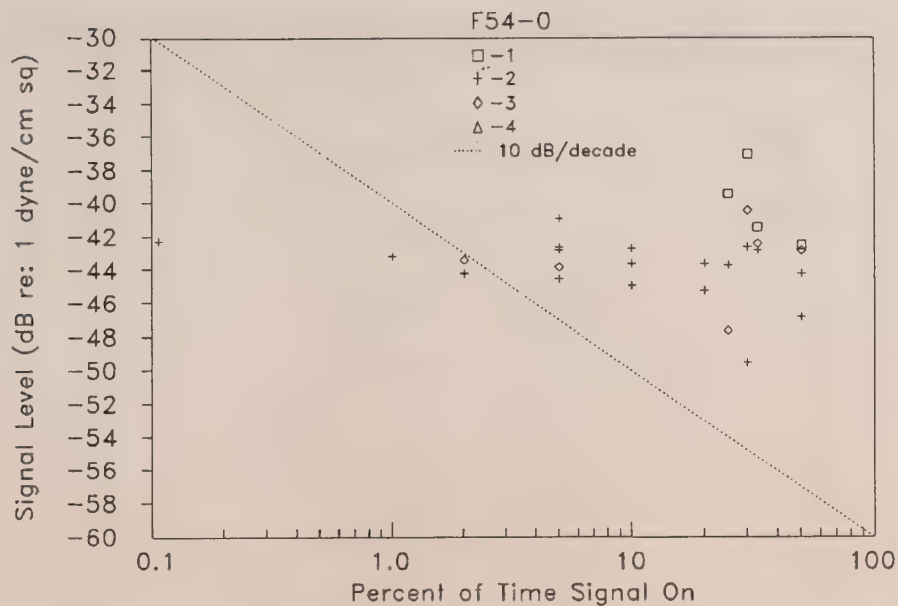


Fig. F54-0. The effect of duty cycle (percent of time signal is on) on quiet pure tone thresholds in *Carassius auratus* (goldfish).

- 1- 300 Hz
- 2- 500 Hz
- 3- 1000 Hz
- 4- 1500 Hz

Reference:

Popper, A.N. (1972) Auditory threshold in the goldfish (*Carassius auratus*) as a function of signal duration. J. Acoust. Soc. Amer. 52, 596-602.

Table F54-0. The effect of duty cycle (percent of time signal is on) on quiet pure tone thresholds in *Carassius auratus* (goldfish).

Time Signal On (%)	Time Signal On (msec)	Threshold (dB re: 1 dyne cm ⁻²)			
		1	2	3	4
1	10		-42.3		
2	10		-43.2	-43.4	
5	10		-44.2		
5	20		-44.5	-43.8	
5	30		-42.6		
5	50		-40.9		
10	10		-42.8		
10	20		-44.9		
10	50		-42.7		
10	100		-43.6		
20	20		-42.7		
20	100		-45.2		
25	100	-39.4	-43.6	-47.6	-20.7
30	30		-43.7		
30	300	-37	-42.6	-40.4	-23
33	200	-41.4	-49.5	-42.4	-25
50	100		-42.8		
50	500	-42.5	-46.8	-42.8	-24.1
90	90		-44.2		

Notes:

See Notes for Fig. F51-0. Rise/fall time 2.5 msec for all signals except the 10 msec duration signals (having 1 msec rise/fall times).

These data show that neither signal duration or duty cycle affects pure tone detection thresholds for the goldfish in quiet. Thus, the signal energy at threshold is less for brief than for long duration signals, and in this sense the goldfish can be said to be adapted for detecting short duration signals in the quiet. However, note that the data of Offutt (1967) in Fig. 52-0, Fay and Coombs (1983) in Fig. 50-0, and Hawkins (1981) in Fig. F53-0 show clear effects of signal duration and duty cycle on threshold, and are thus clearly not in accord with the data here.

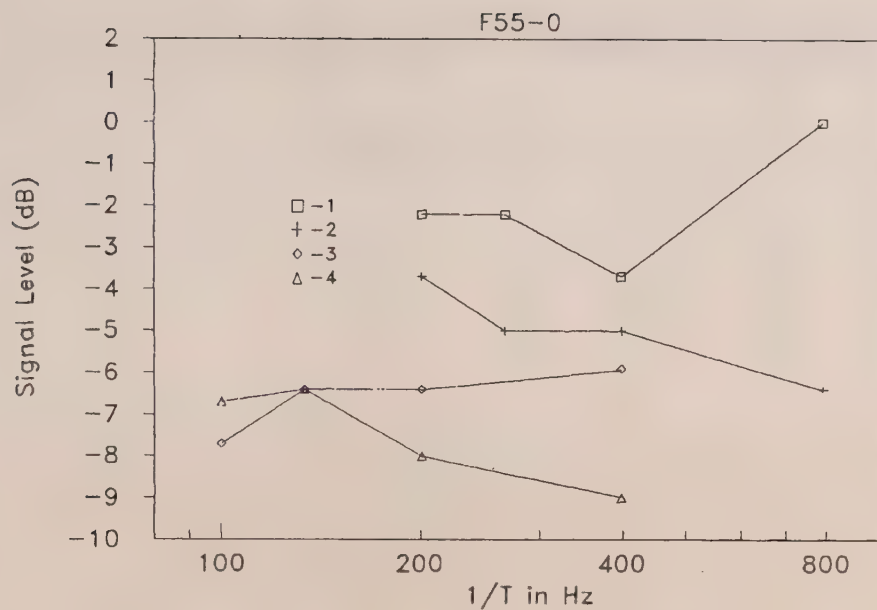


Fig. F55-0. Thresholds for 400 and 800 Hz tones in the presence of cos+ and cos- repetition noise as a function of the spacing between spectral peaks in the noise in *Carassius auratus* (goldfish).

- 1- 800 Hz signal; cos+ noise
- 2- 800 Hz cos-
- 3- 400 Hz cos+
- 4- 400 Hz cos-

Reference:

Fay, R.R., Yost, W.A., Coombs, S. (1983) Psychophysics and neurophysiology of repetition noise processing in a vertebrate auditory system. *Hear. Res.* 12, 31-55.

Table F55-0. Thresholds for 400 and 800 Hz tones in the presence of cos+ and cos- repetition noise as a function of the spacing between spectral peaks in the noise.

1/T (Hz)	Signal Threshold (dB re: 1 dyne cm ⁻²)			
	1	2	3	4
100			-7.7	-6.7
133			-6.4	-6.4
200	-2.2	-3.7	-6.4	-8
267	-2.2	-5		
400	-3.7	-5	-5.9	-9
800	0	-6.4		

Notes:

Repetition noise (sometimes referred to as cosine noise, comb-filtered noise, rippled noise, etc) is produced by splitting a white noise source into two identical channels. One channel is delayed by T sec, and attenuated by A dB relative to the other. The two channels are then added to produce cos+ noise, or subtracted to produce cos- noise. The amplitude spectrum of repetition noise varies sinusoidally as a function of frequency. For cos+ noise, the first peak in the spectrum above zero Hz is at 1/T Hz, where T is the delay used in creating the noise. Successive spectral peaks are separated by 1/T Hz. For cos- noise, the first spectral minimum above zero Hz occurs at 1/T Hz. Humans percieve cos+ repetition noise to have a pitch equal to a pure tone of 1/T Hz.

In this experiment, repetition noise was used as a masker for pure tones. The delay was varied so that the signal always fell on a spectral peak of cos+ noise, and in a spectral trough of cos- noise. The difference in the masking effect of cos+ and cos- noise as a function of delay is a measure of the frequency resolving power of the auditory system (see Pickles, 1979).

In this figure, the differences between cos+ and cos- maskers is only statistically significant at the largest values of 1/T.

Classical respiratory conditioning using the staircase psychophysical procedure. Means: N=4.

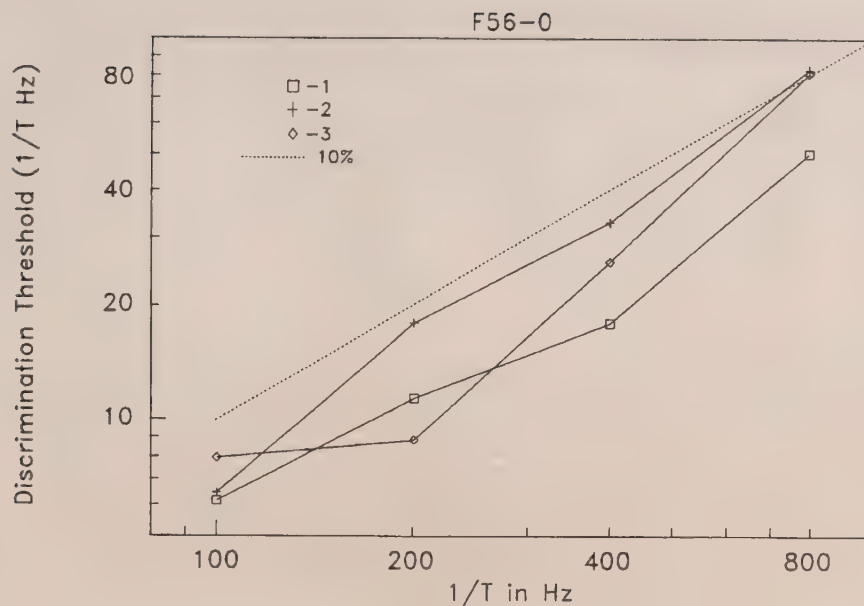


Fig. F56-0. Just discriminable change in repetition noise delay (plotted as $1/T$) as a function of the delay in *Carassius auratus* (goldfish).

- 1- cos+ noise, constant intensity
- 2- cos- noise, constant intensity
- 3- cos+ noise, varying intensity

Reference:

Fay, R.R., Yost, W.A., Coombs, S. (1983) Psychophysics and neurophysiology of repetition noise processing in a vertebrate auditory system. *Hear. Res.* 12, 31-55.

Table F56-0. Just discriminable change in repetition noise delay (plotted as $1/T$) as a function of the delay.

$1/T$ (Hz)	JND for $1/T$ (Hz)		
	1	2	3
100	6.2	6.5	8
200	11.5	18	8.9
400	18	33	26
800	50	83	81

Notes:

See Notes for Fig. F55-0.

This is analagous to a pitch discrimination experiment since human observers percieve a change in pitch accompanying a change in repetition noise delay. Repetition noise pulses were continuously presented 800 msec in duration, once per sec, and the animals conditioned to respond to a change in the delay, T , used in creating the noise. The "constant intensity" condition was one in which the overall intensity of the noise remained unchanged. In the "varying intensity" condition, each successive burst of repetition noise was presented at a different intensity, drawn at random from a rectangular distribution of intensities with a range of 10 dB. This was a control for the possibility that the delay discrimination was based on a possible correlated loudness change. Overall noise level about 45 dB SL.

Compare these thresholds with pure tone frequency discrimination thresholds for the goldfish (Fig. F38-0).

Classical respiratory conditioning using the staircase psychophysical procedure.

Means: $N=4$.

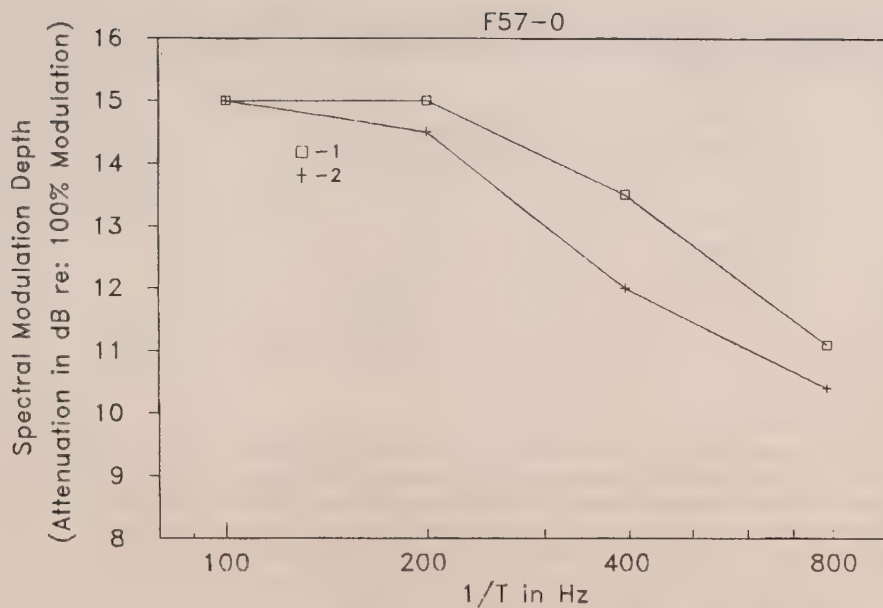


Fig. F57-0. Spectral modulation depth (attenuation in delayed channel) at threshold for detecting a 20% change in repetition noise delay as a function of delay, in *Carassius auratus* (goldfish).

- 1- cos+ noise
- 2- cos- noise

Reference:

Fay, R.R., Yost, W.A., Coombs, S. (1983) Psychophysics and neurophysiology of repetition noise processing in a vertebrate auditory system. *Hear. Res.* 12, 31-55.

Table F57-0. Spectral modulation depth (attenuation in delayed channel) at threshold for detecting a 20% change in repetition noise delay as a function of delay, in *Carassius auratus* (goldfish).

1/T (Hz)	Attenuation (dB)	
	1	2
100	15	15
200	15	14.5
400	13.5	12
800	11.1	10.4

Notes:

See Notes for Fig. F55-0.

This is analogous to a "pitch strength" experiment with human observers (Yost and Hill, 1978). The animals are presented with a detectable (20% change) difference in repetition noise delay, and the spectral modulation depth required to maintain this discrimination at threshold levels is determined as a function of delay. These data show that the goldfish "tolerates" the reduction in spectral modulation best at long delays (1/T from 100 to 200 Hz). By this definition, "pitch strength" declines toward the higher values of 1/T. Differences between cos+ and cos- are not robust.

Classical respiratory conditioning using the staircase psychophysical procedure.
Means: N=4.

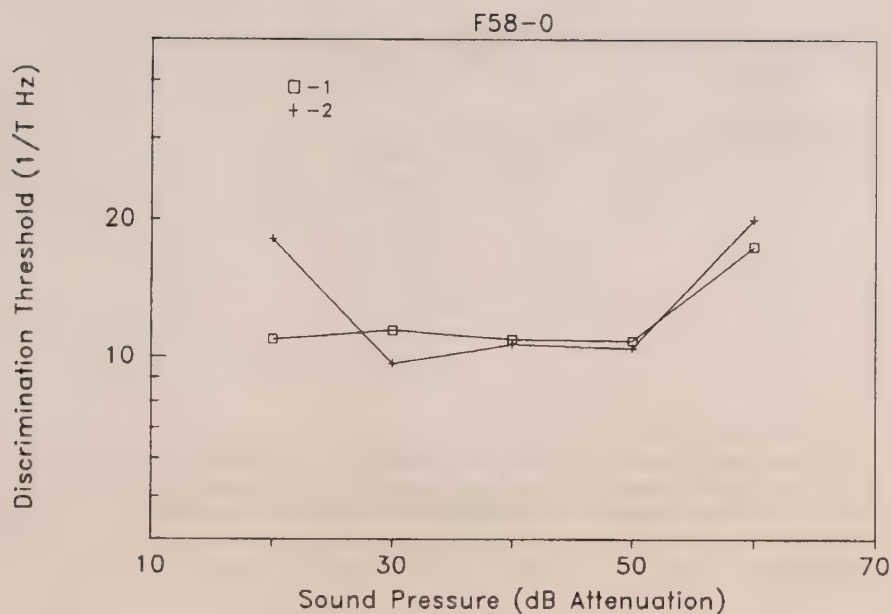


Fig. F58-0. Delay discrimination thresholds at $T=5$ msec for cos+ and cos- repetition noise as a function of overall noise level in *Carassius auratus* (goldfish).

1- cos+ noise
2- cos- noise

Reference:

Fay, R.R., Yost, W.A., Coombs, S. (1983) Psychophysics and neurophysiology of repetition noise processing in a vertebrate auditory system. *Hear. Res.* 12, 31-55.

Table F58-0. Delay discrimination thresholds at T=5 msec for cos+ and cos-repetition noise as a function of overall noise level.

Attenuation (dB)	JND for 1/T (Hz)	
	1	2
20	11	18.2
30	11.5	9.7
40	11	10.7
50	10.9	10.5
60	17.5	20.1

Notes:

See Notes for Fig. F55-0.

This experiment measures how the delay discrimination threshold (for the case of 1/T= 200 Hz) varies as a function of the overall intensity of the repetition noise.

Attenuation of 20 dB corresponds to -10 dB re: 1 dyne cm⁻² Hz⁻¹ sound pressure (about 45 dB sensation level).

Means: N=4.

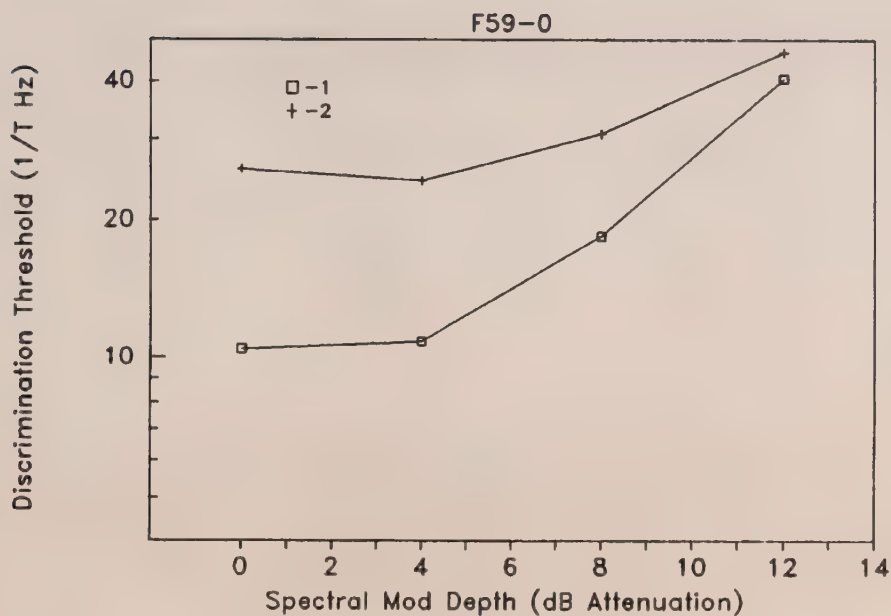


Fig. F59-0. Delay discrimination thresholds at $T=5$ msec for cos+ and cos- repetition noise as a function of spectral modulation depth in *Carassius auratus* (goldfish).

- 1- cos+ noise
- 2- cos- noise

Reference:

Fay, R.R., Yost, W.A., Coombs, S. (1983) Psychophysics and neurophysiology of repetition noise processing in a vertebrate auditory system. *Hear. Res.* 12, 31-55.

Table F59-0. Delay discrimination thresholds at T=5 msec for cos+ and cos-repetition noise as a function of spectral modulation depth.

Attenuation (dB)	JND for 1/T (Hz)	
	1	2
0	10.5	26
4	10.9	24.5
8	18.5	31
12	41	47

Notes:

See Notes for Fig. F55-0.

This experiment measures how the delay discrimination threshold (for the case of $1/T = 200$ Hz) varies as a function of spectral modulation depth. Modulation depth is defined in terms of the attenuation (A) of the delayed noise channel relative to the undelayed channel. Note that at an attenuation of 0 dB, there is a maximum peak-trough amplitude difference (greater than 20 dB). At 8 dB attenuation, the amplitude difference between a spectral peak and a trough is about 7.3 dB.

Noise signal presented about 45 dB sensation level. Means: N=4.

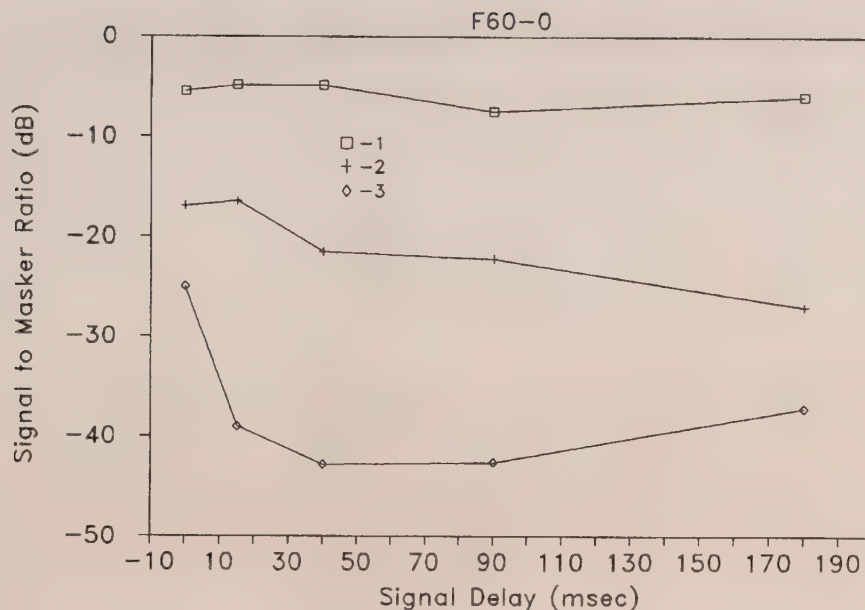


Fig. F60-0. Tone-on-tone masking as a function of the temporal position of the signal in the masker in *Carassius auratus* (goldfish) (Fay and Coombs, 1988).

- 1- 250 Hz masker, 250 Hz signal
- 2- 500 Hz masker, 250 Hz signal
- 3- 1000 Hz masker, 250 Hz signal

Reference:

Fay, R.R., and Coombs, S.L. (1988) Psychophysics and neurophysiology of frequency selectivity and masking in the goldfish. In H. Duifhuis, J. Horst, and H. Wit (eds), Basic Issues in Hearing. Academic Press: New York.

Table F60-0. Tone-on-tone masking as a function of the temporal position of the signal in the masker in *Carassius auratus* (goldfish) (Fay and Coombs, 1988).

Signal Delay (msec)	Signal-to-Masker Ratio (dB)		
	1	2	3
0	-5.5	-17	-25
15	-4.9	-16.5	-39
40	-4.9	-21.5	-42.8
90	-7.5	-22.2	-42.6
180	-6	-27	-37.2

Notes:

Classical respiratory conditioning using a tracking procedure. Maskers (200 msec tone bursts with 10 msec rise/fall times) were presented continuously repeating at one per sec. The signal was a 20 msec duration 250 Hz tone burst at about 10 dB re: 1 dyne cm^{-2} with 10 msec rise/fall times which was added to the repeating masker at different times relative to masker onset (signal delay times). At zero msec signal delay, the signal and masker onsets were simultaneous. At 180 msec signal delay, the signal and masker offsets were simultaneous. When both signal and masker were 250 Hz, the signal was added in phase with the masker. Thresholds were defined by tracking on masker level. Means: N=4.

Note that these data are similar to the data from comparable experiments on human observers. In both species, there is little effect of signal delay when the masker and signal frequencies are equal, and a robust effect when the masker is well above the signal in frequency. An explanation for this effect is not yet clear, but one consequence is that psychophysical tuning curves derived using these procedures are broadly tuned when signal and masker come on together, but are more sharply tuned when the signal is temporally centered in the masker.

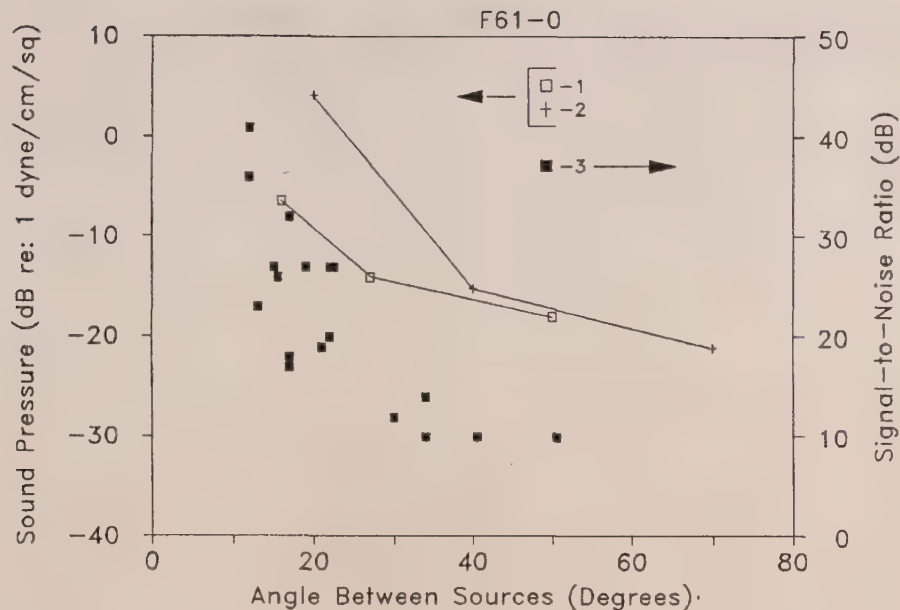


Fig. F61-0. Thresholds for the detection of angular change in the direction of a source as a function of signal level or signal-to-noise ratio in *Gadus morhua* (cod).

- 1- Vertical plane or elevation (signal level) (Hawkins and Sand, 1977)
- 2- Horizontal plane or azimuth (signal level) (Chapman and Johnstone, 1974)
- 3- Horizontal plane or azimuth (signal-to-noise ratio) (Buwalda, 1981)

References:

- Buwalda, R.J.A. (1981) Segregation of directional and nondirectional acoustic information in the cod. In W.N. Tavolga, A.N. Popper, and R.R. Fay (eds), *Hearing and Sound Communication in Fishes*. Springer-Verlag: New York, pp. 139-178.
- Chapman, C.J. and Johnstone, A.D.F. (1974) Some auditory discrimination experiments on marine fish. *J. Exp. Biol.* 61, 521-528.
- Hawkins, A.D. and Sand, Q. (1977) Directional hearing in the median vertical plane by the cod. *J. Comp. Physiol.* 122, 1-8.

Table F61-0. Thresholds for the detection of angular change in the direction of a source as a function of signal level or signal-to-noise ratio in *Gadus morhua* (cod).

Angle Between Sources (Deg)	Threshold Level for Discrimination (dB re: 1 dyne cm ⁻²)		S/N 3
	1	2	
12			41
12			36
13			23
15			27
15.5			26
16	-6.5		
17			32
17			18
17			17
19			27
20		4.1	
21			19
22			27
22			20
22.5			27
27	-14.1		
30			12
34			14
34			10
40		-15.2	
40.5			10
50	-18		
50.5			10
70		-21.2	

Notes:

These are minimum audible angle measurements determined as a function of signal level (#1 and #2), or as a function of signal-to-noise ratio (#3). It is clear that the cod is capable of a directional discrimination acuity of at least 16° vertically, and 12-20° horizontally when the signal level is intense enough.

1-2- Classical cardiac conditioning using the staircase psychophysical procedure. Underwater projectors (J9) in an acoustic free field. Signals were 110 Hz tones, 500 msec duration, 75 msec rise/fall times. 1- Medians: N=2. 2- Medians: N=3.

3- Classical cardiac conditioning using the staircase psychophysical procedure. Experiments were carried out in the laboratory using a three-dimensionally synthesized sound field (three orthogonal pairs of underwater loudspeakers) in which the impedance of the sound field in the region of the fish (the ratio of pressure to particle velocity) could be manipulated over a wide range. The signal was a 105 Hz tone presented at a very low pressure-to-velocity ratio (large motional component compared with the far field case). The azimuth of particle motion could be manipulated precisely in the synthesized sound field. The noise was wide band and effectively omnidirectional. The S/N was specified as the signal velocity in the horizontal plane relative to the noise spectrum level of the velocity of the components in the horizontal plane. N=15.

Hearing in Amphibians and Reptiles

The amphibians include the urodeles (salamanders and newts), the apodans (caecilians), and the anurans (frogs and toads). Psychophysical hearing data exist only for the anurans. The anurans are of particular experimental interest because many of them vocalize during mating and other social interactions, and the detection, discrimination, and localization of these species specific vocalizations are of obvious importance for survival of the species. Many of the studies included in this section were carried out using the natural tendency of many anurans to orient to or otherwise respond to sounds broadcast in a more or less natural setting. Many of these studies are not strictly psychophysical studies since the natural tendency of the animals to respond in any given experimental situation was generally beyond the control of the experimenter. In these cases, "thresholds" reflect the sensitivity of the response as well as the sensitivity of the auditory system. The exceptions to this are new experiments using a reflex modification procedure to study anuran hearing in a more strict, psychophysical paradigm (A1-0, A9-0).

The outer and middle ears of anurans generally consist of a large tympanic membrane nearly flush with the skin surface, and a columella (or stapes) which acts as an impedance transformer as it transmits motions of the tympanic membrane to the fluid-filled inner ear. This is the general "plan" for most all terrestrial vertebrates. The middle ear air-spaces open widely to the mouth cavity via large eustachian tubes. This wide pathway of communication between the two ears and the mouth, lungs, (and possibly the endolymphatic sac which is located dorsally on the animal's neck and upper back) makes possible several potential pathways of sound both to the outer and inner surface of the tympanic membrane. Evidence exists that the ears of some anurans operate both as pressure receivers and pressure gradient receivers in certain frequency ranges. Since pressure gradients are vector quantities, the ear operating in this mode is inherently directional.

Anurans also possess three otolith organs; the saccule, utricle, and lagena. Evidence exists that the saccule is highly sensitive to low frequency vertical vibrations of the head, and may function in air as a substrate vibration detector. When anurans "call," a portion of the energy of the call enters the ground and is transmitted via waves that are not unlike water surface waves. Underwater, the saccule may detect sound in much the same way that the saccule and other otolith organs of the fishes detect sound; i.e. operating as an accelerometer. Many anuran species are mostly submerged in water when they advertise vocally for mates, and when they orient to and seek out the sources of these advertisement calls. Of course, anurans are entirely aquatic in the tadpole stage, and would be expected to have fish-like hearing mechanisms at this time of life.

The auditory portions of the anuran inner ear include the **basilar papilla** and the **amphibian papilla**. These are two, independent organs which operate in different but overlapping frequency ranges. The amphibian

papilla responds in a frequency range from below 100 to just over 1000 Hz, and the basilar papilla responds from several hundred to several thousand Hz, depending on the species. The amphibian papilla performs a frequency analysis analogous to that performed by the cochlea of birds and mammals, and shows other physiological properties similar to the cochlea. The basilar papilla seems to be a single-tuned structure.

Reviews of the structures and functions of the anuran auditory system can be found in Capranica (1965), Popper and Fay (1980), Capranica and Moffat (1983), Lewis, Leverenz, and Bialek (1985), and Wever (1985).

Reptiles have been almost entirely neglected in behavioral studies of hearing, and I am aware of only one report in the literature - on the hearing sensitivity of a turtle (A6-0). The reptile outer and middle ear is similar to that described for the anurans, except that the tympanic membrane may be recessed below the skin in some species. The auditory portions of the reptile inner ear include a single organ, the basilar papilla. There is considerable diversity in the size, shape, number of hair cells, and mechanisms of hair cell stimulation among the reptiles. The smallest basilar papillae are found among the iguanids, and the longest among the gekkos, and the caiman. The caiman ear is similar to the bird ear.

Some reptiles vocalize (e.g. gekkos), but many do not. It has been difficult to gain experimental control over the behavior of reptiles for a psychophysical study of hearing. Reviews of the structures and functions of the reptile ears can be found in Wever (1978) and Manley (1981).

Audiograms for the anurans (A1-0 to A5-0) show best sensitivity ranging from about 10 dB to 60 dB SPL, with best sensitivity in the range from 100 to 2000 Hz. It is likely that best sensitivity has been underestimated in most studies making use of unconditioned sound-evoked responses. The sensitivity determined for the bullfrog and green tree frog in Fig. A1-0 are the best estimates we now have for anuran hearing sensitivity.

The one audiogram for a reptile (a turtle) appears in Fig. A6-0. Best sensitivity is about 40 dB SPL at 400 Hz.

Clever field studies making use of unconditioned sound-evoked behavior have estimated the intensity discrimination threshold of a neotropical tree frog to be about 4.5 dB (Fig. A7-0).

The sound-evoked calling behavior of the bullfrog depends on sound intensity, with 80 to 90 dB optimal (A8-0). Background noise in the region of 3000 Hz is most effective in suppressing vocalization (Fig. A13-0).

Critical masking ratios in the bullfrog and green tree frog are unlike those in fishes, most birds and most mammals in that there may be certain frequency regions of acute sensitivity flanked by frequency regions of poor sensitivity. In the green tree frog, the two areas of best signal detection in noise correspond roughly to the peak sensitivity regions of the amphibian and basilar papillae (A9-0). Critical masking ratios for two-tone complexes can be significantly below (about 10 dB) those for pure tones if the two tones are harmonically related (Fig. A9-0).

Field experiments have estimated critical masking ratios and critical bandwidths (Figs. A10-0 to A12-0).

Anurans are able to localize and seek out sound sources with an accuracy of about 10 to 20 degrees in both azimuth and elevation.

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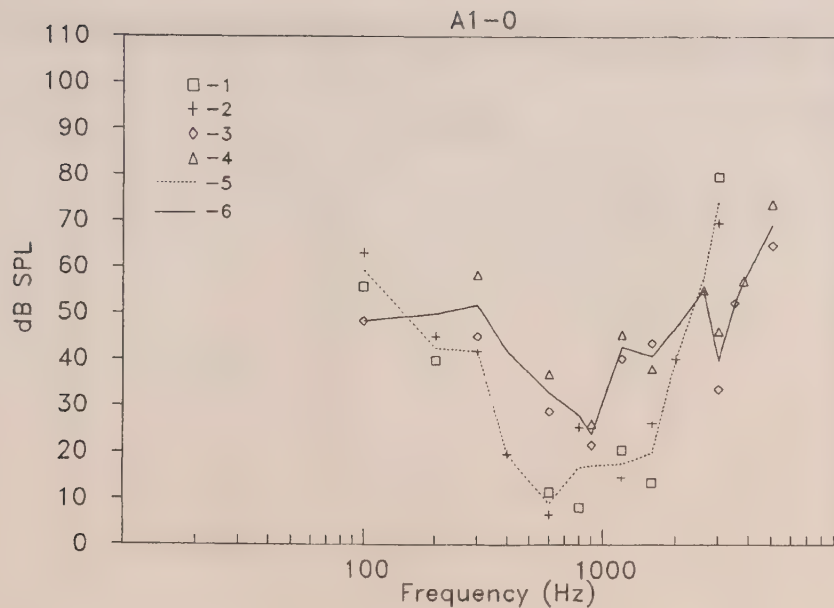


Fig. A1-0. Behavioral audiograms using the reflex inhibition method for two anuran species (Megela Simmons, Moss, and Daniel, 1985)

- 1- Animal 1
- 2- Animal 2
- 5- Mean
- Rana catesbeiana* - bullfrog
- 3- Animal 1
- 4- Animal 2
- 6- Mean
- Hyla cinerea* - green tree frog

Reference:

Megela Simmons, A., Moss, C.F., and Daniel, K.M. (1985) Behavioral audiograms of the bullfrog (*Rana catesbeiana*) and the green tree frog (*Hyla cinerea*). J. Acoust. Soc. Amer. 78, 1236-1244.

Table A1-0. Behavioral audiograms using the reflex inhibition method for two anuran species (Megela Simmons, Moss, and Daniel, 1985).

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
100	55.8	63.1	48.4		59.5	48.4
200	39.9	45.1			42.5	
300		41.8	45.1	58.5	41.8	51.8
400		19.7			19.7	
600	11.5	6.6	28.8	36.9	9.1	32.9
800	8.2	25.4			16.8	
900			21.6	26.2		23.9
1200	20.5	14.7	40.3	45.5	17.6	42.9
1600	13.5	26.2	43.6	38	19.9	40.8
2000		40.2			40.2	
2600				55.1		55.1
3000	79.6	69.7	33.6	46.2	74.7	39.9
3500			52.3			52.3
3800				57.2		57.2
5000			64.8	73.8		69.3

Notes:

Thresholds were determined with the reflex inhibition method (see Yerkes, 1904, 1905) using the method of constant stimuli. In this paradigm, shock is used to elicit a movement reflex. Presentation of a pure tone before the shock (400 msec before for bullfrog, 200 msec before for green tree frog) tends to reduce the shock-evoked reflex. Pure tones were 400 msec duration for bullfrog, and 200 msec for green tree frog, with 10 msec rise/fall times. The sound pressure level producing a reflex reduction of 10% was interpolated from reflex reduction functions of sound pressure level. These functions have slopes averaging 0.3 to 0.6 % per dB.

These are the only audiograms for anurans determined using a true psychophysical method. See Fig. A9-0 for masked thresholds using the same methods.

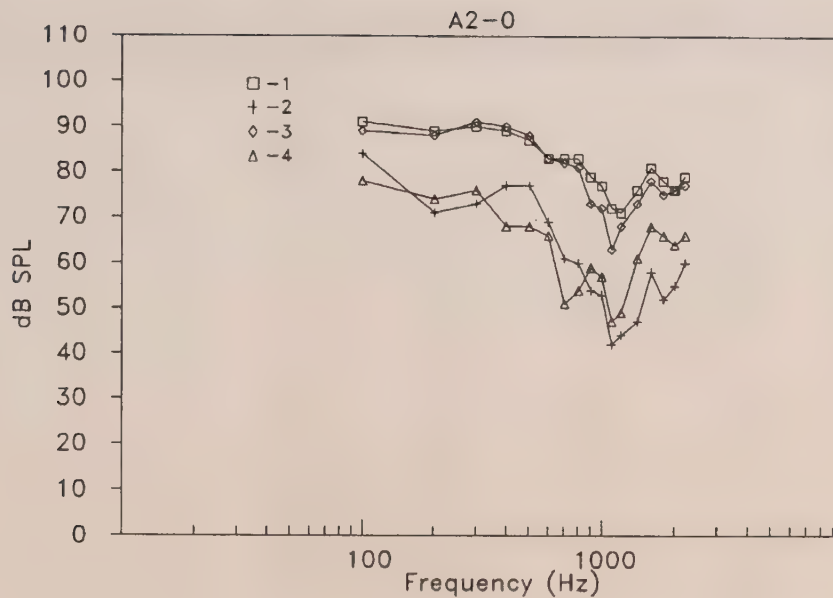


Fig. A2-0. Audiograms for male and female grass frogs (*Rana t. temporaria* L.) from Brzoska, Walkowiak and Schneider (1977) using the sound-evoked electrodermal response.

- 1- Males, mean, N=12
- 2- Males, most sensitive threshold value
- 3- Females, mean, N=17
- 4- Females, most sensitive threshold value

Reference:

Brzoska, J., Walkowiak, W. and Schneider, H. (1977) Acoustic communication in the grass frog (*Rana t. temporaria* L.): Calls, auditory thresholds and behavioral responses. *J. Comp. Physiol.* 118, 173-186.

Table A2-0. Audiograms for male and female grass frogs (*Rana t. temporaria* L.) from Brzoska, Walkowiak and Schneider (1977) using the sound-evoked electrodermal response.

Frequency (Hz)	dB SPL			
	1	2	3	4
100	91	84	89	78
200	89	71	88	74
300	90	73	91	76
400	89	77	90	68
500	87	77	88	68
600	83	69	83	66
700	83	61	82	51
800	83	60	81	54
900	79	54	73	59
1000	77	53	72	57
1100	72	42	63	47
1200	71	44	68	49
1400	76	47	73	61
1600	81	58	78	68
1800	78	52	75	66
2000	76	55	76	64
2200	79	60	77	66

Notes:

These thresholds are for the unconditioned electrodermal response recorded between two alligator clip electrodes positioned at the neck and just above the anus. The potentials between these points were low-pass filtered at 0.5 Hz. Response latencies ranged from 2 to over 20 sec. Pure tone signals were 15-20 sec in duration, spaced at least 1 min apart. During testing, the animals were immobilized with a 2% solution of Succinyl-Asta.

These thresholds likely do not indicate optimal absolute sensitivity since they depend on the response threshold for the electrodermal response. However, they may define relative sensitivity at different frequencies.

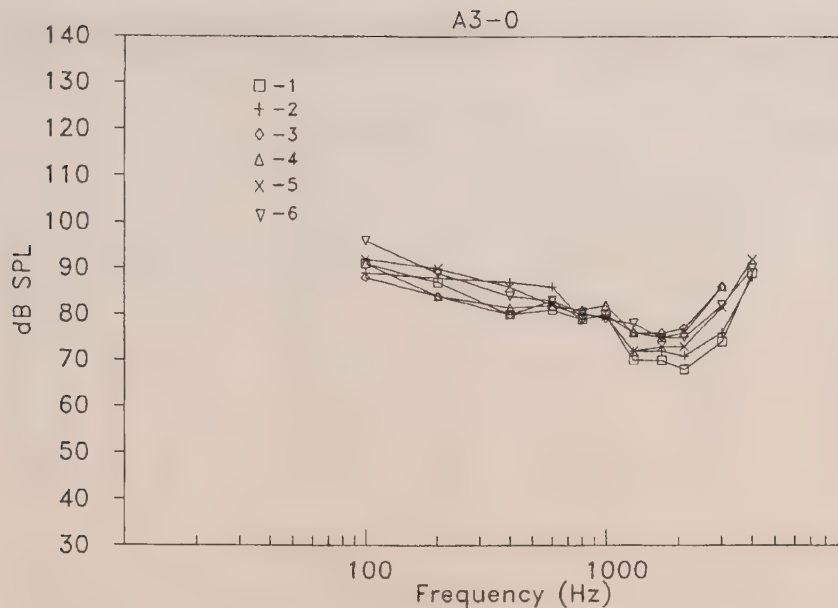


Fig. A3-0. Audiograms for males and females of three anuran species (European water frogs) determined using the unconditioned, sound-evoked electrodermal response.

- 1- *Rana lessonae*, female
- 2- *Rana lessonae*, male
- 3- *Rana ridibunda*, female,
- 4- *Rana ridibunda*, male
- 5- *Rana "esculenta,"* female
- 6- *Rana "esculenta,"* male

Reference:

Brzoska, J. (1980) Quantitative studies on the elicitation of the electrodermal response by calls and synthetic acoustical stimuli in *Rana lessona* Camerano, *Rana r. ridibunda* Pallas and the hybrid *Rana esculenta* L. (Anura, Amphibia). Behav. Processes 5, 113-141.

Table A3-0. Audiograms for males and females of three anuran species (European water frogs) determined using the unconditioned, sound-evoked electrodermal response.

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
100	91	89	88	91	92	96
200	87	88	84	84	90	89
400	80	87	80	81.5	86	84
600	81	86	83	82	82	83
800	79	79	79	81	80	80.5
1000	80	80	80	82	79.5	79
1300	70	72	76	76	72	78
1700	70	72	76	75	73	75
2100	68	71	77	76	73	75
3000	74	76	86	86	81.5	82
4000	89	88			92	90

Notes:

Thresholds are for the unconditioned, sound-evoked electrodermal response. During testing, the animals were immobilized with a 2% solution of Succinyl-Asta or Curarin Asta. Each stimulus was a series of 50 msec tone pulses, 5 msec rise/fall times, repeated 10 per sec at the indicated frequency, lasting for 15 sec. Responses were observed during and up to 5 sec following the 15 sec stimulus. For all groups, data are means for 5 animals.

These thresholds were obtained during October, just after the normal mating (calling) period. Thresholds were also obtained at the end of May, during the mating period. These thresholds were slightly higher but not systematically different from those shown here. Thresholds were also obtained in response to the various calls of the different species.

Note that *Rana "esculenta"* is the hybrid of the other two species used, and that *Rana ridibunda* is the largest of the three frogs.

These thresholds likely do not indicate optimal absolute sensitivity since they depend on the response threshold for the electrodermal response. However, they may define relative sensitivity at different frequencies.

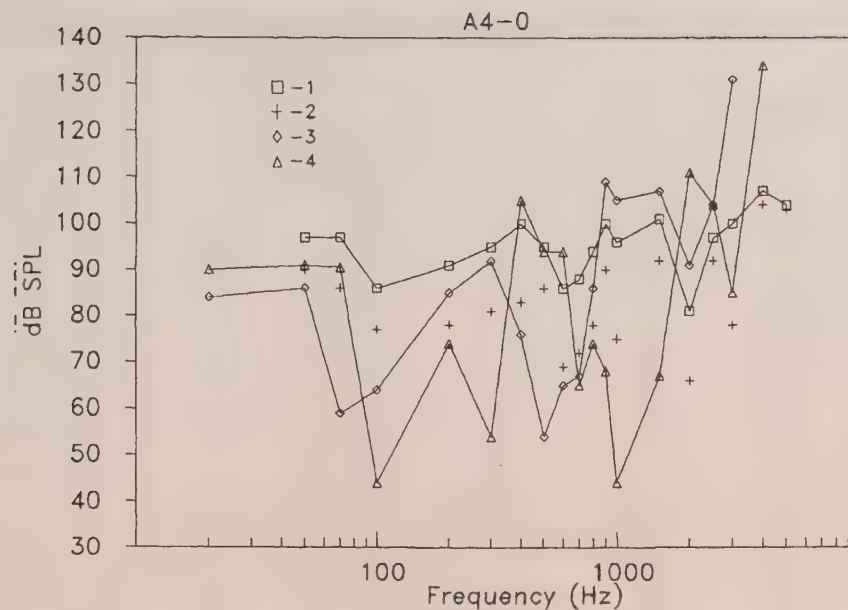


Fig. A4-0. Audiograms for two anuran species determined using the electrodermal response.

1-2 *Hyla cinerea* - green tree frog (Weiss and Strother, 1965)

1- Mean for 7 subjects

2- Lowest threshold value

3-4 *Rana catesbeiana* - bullfrog (Strother, 1962)

3- Male, N=1

4- Female, N=1

References:

Strother, W.F. (1962) Hearing in frogs. J. Aud. Res. 2, 279-286.

Weiss, B.A., and Strother, W.F. (1965) Hearing in the green treefrog (*Hyla cinerea*). J. Aud Res. 5, 297-305.

Table A4-0. Audiograms for two anuran species determined using the electrodermal response.

Frequency (Hz)	dB SPL			
	1	2	3	4
20			84	90
50	97	90	86	91
70	97	86	59	90.5
100	86	77	64	44
200	91	78	85	74
300	95	81	92	54
400	100	83	76	105
500	95	86	54	94
600	86	69	65	94
700	88	72	67	65
800	94	78	86	74
900	100	90	109	68
1000	96	75	105	44
1500	101	92	107	67
2000	81	66	91	111
2500	97	92	104	
3000	100	78	131	85
4000	107	104		134
5000	104	103		

Notes:

These thresholds were determined using the unconditioned, sound-evoked electrodermal response ("galvanic skin response") along with a modified method of limits. Two electrodes (Michel surgical clips) were clipped to the skin, one on the neck between the ears, and the other just above the anus. Signals were tones with 200 msec rise/fall times. Thresholds were obtained using visual inspection of response as recorded on a strip-chart recorder.

These thresholds likely do not indicate optimal absolute sensitivity since they depend on the response threshold for the electrodermal response. However, they may define relative sensitivity at different frequencies.

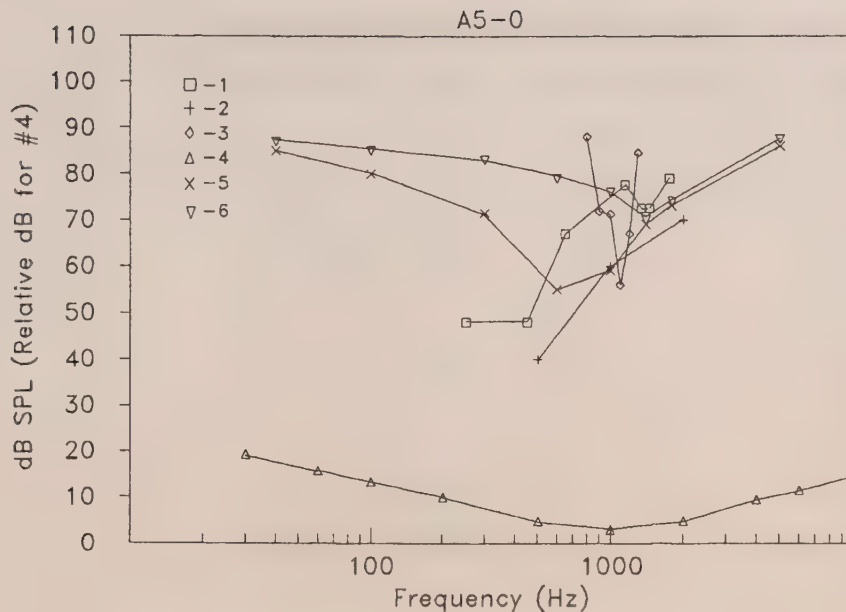


Fig. A5-0. Auditory sensitivity in several anuran species using several different techniques.

- 1- *Eleutherodactylus coqui* - neotropical tree frog (Zelick and Narins, 1982)
- 2- *Eleutherodactylus coqui* - neotropical tree frog (Zelick and Narins, 1982)
- 3- *Eleutherodactylus coqui* - neotropical tree frog (Narins and Capranica, 1978)
- 4- *Rana clamitans* - green frog, and *Rana pipiens* - leopard frog (Kleerekoper and Sibabin, 1959)
- 5- *Rana temporaria* - grass frog, and *Rana esculenta* - European water frog (Volkmer, 1959)
- 6- Same as #5, eardrums excised

References:

- Kleerekoper, H., and Sibabin, K. (1959) A study of hearing in frogs (*Rana pipiens* and *Rana clamitans*). *Z. vergl. Physiol.* 41, 490-499.
- Narins, P.M. and Capranica, R.R. (1978) Communicative significance of the two-note call of the Treefrog *Eleutherodactylus coqui*. *J. Comp. Physiol.* 127, 1-9.
- Zelick, R.D. & Narins, P.M. (1982) Analysis of acoustically evoked call suppression behavior in a neotropical treefrog. *Anim. Behav.* 30, 728-733.
- Volkmer, E. (1959) Über die Wirkung von Tönen verschiedener Frequenz auf mit gamma-Hexachlorcyclohexan vergifte Frösche (Luft- u. Knochenleitung). *Acta Biol. Med. Germ.* 3, 307-310.

Table A5-0. Auditory sensitivity in several anuran species.

Frequency (Hz)	dB SPL (or with an arbitrary reference, #4)					
	1	2	3	4	5	6
30				19.4		
40					85	87
60				15.9		
100				13.4	80	85
200				10		
250	48					
300					71.5	83
450	48					
500		40		4.8		
600					55	79
650	67					
800			88			
900			71.8			
1000		60	71.2	3	59	76
1100			56			
1150	77.5					
1200			67			
1300			84.5			
1350	72.5					
1400					69	70
1450	72.5					
1750	79					
1800					73	74
2000		70		4.8		
4000				9.5		
5000					86	87.5
6000				11.5		
10000				14.5		

Notes:

1-2- Tendency to suppress calling during sound broadcast. Plotted are the sound pressure levels (calculated from measures 1 meter from the source) of tone or octave band noise bursts (0.7 to 1.1 sec duration, 1.1 to 1.7 silent period intervals) required to reduce calling by a criterion amount. N=11. Medians of points plotted by Zelick and Narins (1982).

1- Tones

2- Octave band noise

3- Same methods as #1 and #2, carried out during May, 1973 and August 1974. N=1. 100 msec tone bursts repeated once per 4 sec.

4- Unconditioned change in respiratory pattern evoked by tone presentation. N=3. Thresholds presented as a parabolic function best fit to data not given. Thresholds given in terms of "...the output current of the oscillator (V^2).\" I interpreted these as voltage squared, and converted them to decibels re: 1 volt using $10 \log(V^2)$.

5- Unconditioned response to light is decreased during sound presentation. N=20.

6- Same methods as for #5 but with tympanic membranes excised. N=20.

All of these thresholds likely do not indicate optimal absolute sensitivity since they depend on the response threshold for the particular response used. However, they may define relative sensitivity at different frequencies.

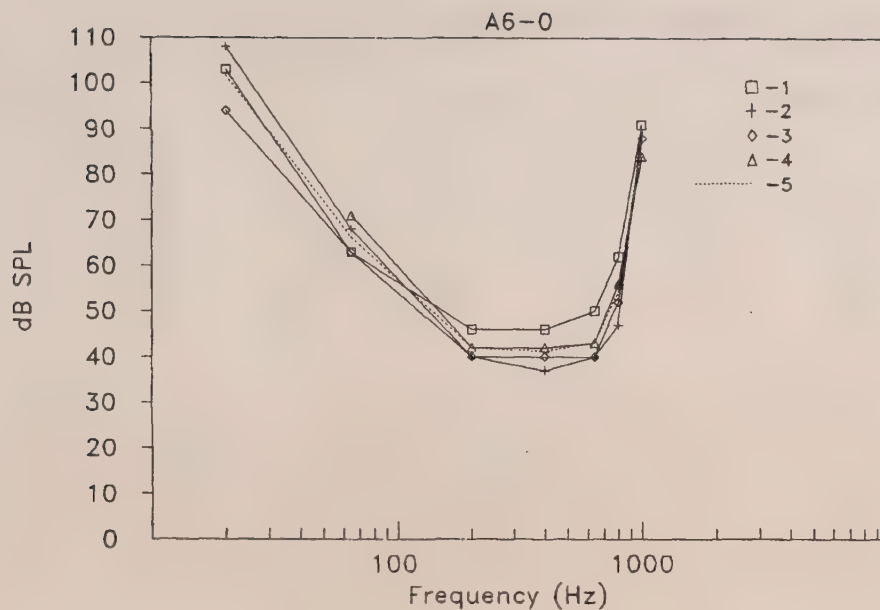


Fig. A6-0. Audiogram for *Pseudemys* sp. (a turtle) (Patterson, 1966).

- 1- Subject 1
- 2- Subject 2
- 3- Subject 3
- 4- Subject 4
- 5- Mean over four subjects

Reference:

Patterson, W.C. (1966) Hearing in the turtle. *J. Aud. Res.* 6, 453-464.

Table A6-0. Audiogram for *Pseudemys* sp. (a turtle) (Patterson, 1966).

Frequency (Hz)	dB SPL				
	1	2	3	4	5
20	103	108	94		101.7
64	63	68	63	71	66.3
200	46	40	40	42	42
400	46	37	40	42	41.3
640	50	40	40	43	43.3
800	62	47	52	56	54.3
1000	91	90	88	84	88.3

Notes:

This species is likely *Pseudemys scripta*.

Instrumental shock avoidance conditioning using the method of limits. Animals had pins implanted in the lower jaw, allowing both a pathway for shock and an anchor point for a line used to pull the head out. Once the head was pulled out, it tended to stay out. Animals were trained to withdraw the head in the presence of a tone in order to avoid shock.

This paper also reports thresholds for the detection of vibration (acceleration) on the carapace, and the effect on auditory sensitivity of cutting the columella. Cutting the columella had no effect on vibration thresholds (generally -10 to 10 dB re: 1 in sec⁻²), but resulted in a loss of sensitivity to sound, reaching over 60 dB above 200 Hz, and reducing toward zero at 20 Hz.

To my knowledge, this is the only psychophysical study of hearing in a reptile.

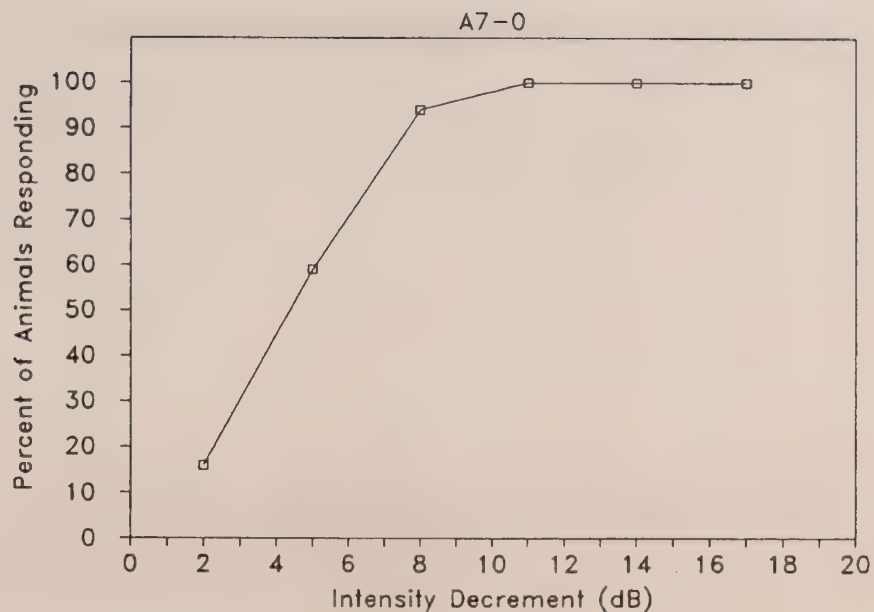


Fig. A7-0. The effect of a tone intensity decrement on the vocal response of *Eleutherodactylus coqui* (neotropical tree frog).

Reference:

Zelick, R.D. & Narins, P.M. (1983) Intensity discrimination and the precision of call timing in two species of neotropical treefrogs. *J. Comp. Physiol.* 153-403-412.

Table A7-0. The effect of a tone intensity decrement on the vocal response of *Eleutherodactylus coqui* (neotropical tree frog).

Intensity Decrement (dB)	Percent Animals Responding
2	16
5	59
8	94
11	100
14	100
17	100

Notes:

In field acoustic playback experiments, males of this species tend to suppress normal vocalization during tone burst presentation. In this experiment, a continuous pure tone (1.1 kHz at 75 dB SPL) was amplitude-modulated at 0.4 Hz such that 1-1.5 sec windows of reduced or decremented sound intensity occurred. The depth of the decrement varied from 2 to 17 dB. The number of animals observed to increase response during the decremented window was determined. The author suggests that a threshold intensity discrimination limen is between 3 and 6 dB. Means: N=23.

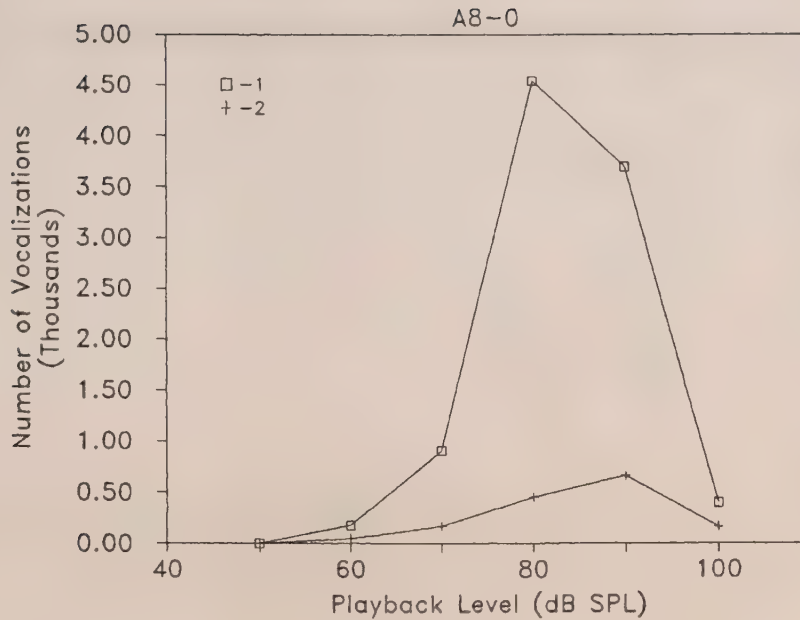


Fig. A8-0. The effect of playback intensity on evoked calling behavior in *Rana catesbeiana* (bullfrog).

- 1- Total evoked calls, all 30 trials
- 2- Total evoked calls, first of 30 trials for each animal

Reference:

Megela Simmons, A. (1984) Behavioral vocal response thresholds to mating calls in the bullfrog, *Rana catesbeiana*. J. Acoust. Soc. Amer. 76, 676-681.

Table A8-0. The effect of playback intensity on evoked calling behavior *Rana catesbeiana* (bullfrog).

Playback Level (dB SPL)	Total Evoked Calls	
	1	2
50	0	0
60	176	47
70	907	170
80	4539	449
90	3697	661
100	399	164

Notes:

Male bullfrogs will vocalize in response to the advertisement calls of male conspecifics. In this laboratory experiment, six adult males were presented with tape recordings of conspecific advertisement calls broadcast at the indicated overall sound pressure levels. Recorded calls (one trial) were five individual croaks separated by 0.5 sec intervals. One 30 trial session at a given intensity was presented every 40 min. Clearly, calls broadcast at 80 dB SPL are the most effective.

Comparing total calls to the calls evoked on the first trial of each session gives an indication of the degree of habituation occurring in this experiment.

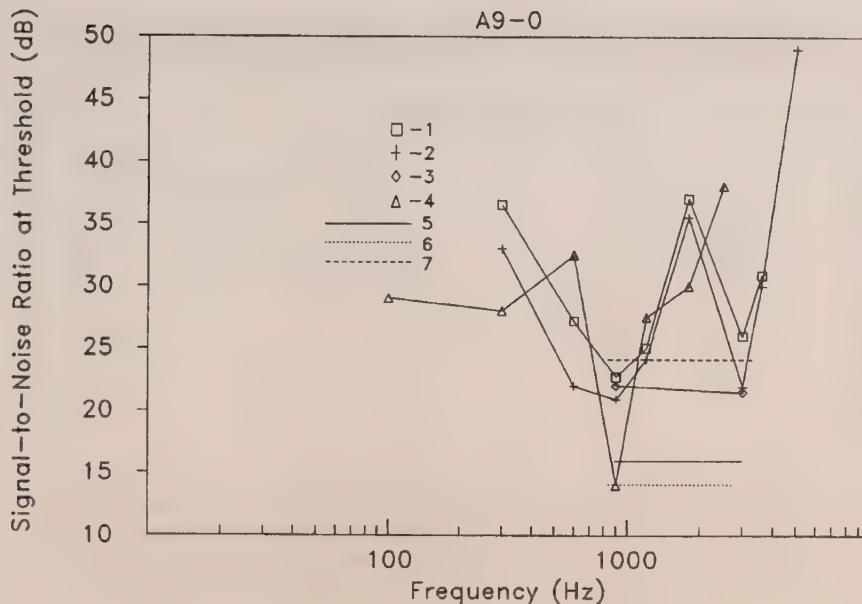


Fig. A9-0. The masking of tones and tone complexes by noise in the auditory system of *Hyla cinerea* (green tree frog), and in *Rana catesbeiana* (bullfrog).

Hyla cinerea - green tree frog

- 1- 25 dB/Hz noise spectrum level (Moss and Megela Simmons, 1986)
- 2- 35 dB/Hz noise spectrum level (Moss and Megela Simmons, 1986)
- 3- 25-55 dB/Hz noise spectrum level (Ehret and Gerhardt, 1980)

Rana catesbeiana - bullfrog

- 4- 25 dB/Hz noise spectrum level (Megela Simmons, 1988a)

Hyla cinerea - green tree frog (Megela Simmons, 1988b)

- 5- Harmonic tone pair 1
- 6- Harmonic tone pair 2
- 7- Inharmonic tone pair

References:

- Ehret, G. & Gerhardt, H.C. (1980) Auditory masking and effects of noise on responses of the green treefrog (*Hyla cinerea*) to synthetic mating calls. *J. Comp. Physiol.* 141, 13-18.
- Megela Simmons, A. (1988a) Masking patterns in the bullfrog (*Rana catesbeiana*), I: Behavioral effects. *J. Acoust. Soc. Amer.* 83, 1087-1092.
- Megela Simmons, A. (1988b) Selectivity for harmonic structure for complex sounds by the green treefrog (*Hyla cinerea*) *J. Comp. Physiol.* 162, 397-403.
- Moss, C.F. and Megela Simmons, A. (1986) Frequency selectivity of hearing in the green treefrog, *Hyla cinerea*. *J. Comp. Physiol.* 159, 257-266.

Table A9-0. The masking of tones and tone complexes by noise in the auditory system of *Hyla cinerea* (green tree frog), and in *Rana catesbeiana* (bullfrog).

Frequency (Hz)	Critical Masking Ratio (dB)						
	1	2	3	4	Tone Pair (Hz)	5	6 7
100				29			
300	36.5	33		28	900 + 3000	16	
600	27.2	22		32.5	828 + 2760		14
900	22.7	20.9	22	14	830 + 3100		24
1200	25	24.1		27.5			
1800	37	35.5		30			
3000	26	21.9	21.5	38			
3600	30.9	30					
5000		49					

Notes:

1-2- These thresholds were determined using the reflex inhibition technique used in Fig. A1-0 (see Notes) to determine audiograms in anurans. Flat spectrum noise was present continuously, and signals were tone bursts with 10 msec rise/fall times presented 200 msec preceding the shock (the reflex-eliciting stimulus). Method of constant stimuli. Threshold defined as a 10% reflex inhibition. The critical masking ratio is the difference (in dB) between the sound pressure level of the tone at threshold and the spectrum level (dB/Hz) of the masking noise. The similarity of curves 1 and 2 indicate that the critical masking ratio is nearly independent of noise level in this intensity range.

1- N=10

2- N=7

3- These masked thresholds were determined using the unconditioned response of females to approach the source of sounds having some similarity to the male mating calls. Tones of fixed intensity were introduced against a continuous broad band noise background, and the noise level increased until the tone failed to be attractive to the animal (i.e. failed to cause an approach). N=19.

4- Same procedure as #1 and 2 above. Masking noise continuous at 25 dB spectrum level. N=1.

5-7- Methods as in #1 and #2 above. Broad band masker at 25 dB spectrum level. This result shows that harmonic complexes (characteristic of anuran vocalizations) are more efficiently detected in a noise background than inharmonic complexes. This is presumably due to central rather than peripheral processing.

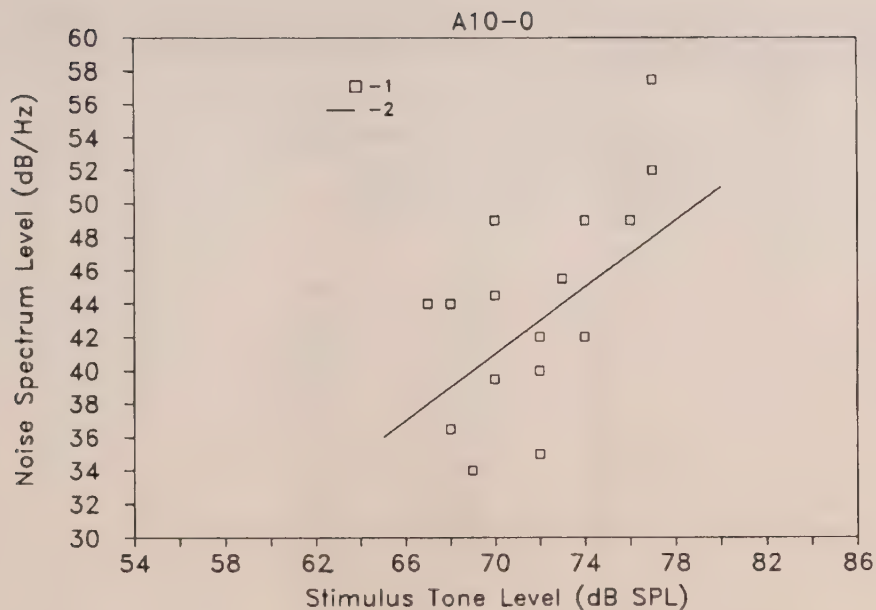


Fig. A10-0. Scatter plot showing the relation between the stimulus tone level used to evoke a vigorous synchronous calling response and the spectrum level of a noise masker required to reduce the response below threshold in *Eleutherodactylus coqui* (neotropical tree frog).

- 1- Data points from individual animals
- 2- Points at which tone power equals total noise power

Reference:

Narins, P.M. (1983) Synchronous vocal response mediated by the amphibian papilla in a neotropical treefrog: Behavioral evidence. *J. Exp. Biol.* 105, 95-105.

Table A10-0. Relation between the stimulus tone level used to evoke a vigorous synchronous calling response and the spectrum level of a noise masker required to reduce the response below threshold.

Stimulus Tone Level (dB)	Noise Spectrum Level (dB/Hz)	
	1	2
67	44	38
68	44	39
68	36.5	39
69	34	40
70	39.5	41
70	44.5	41
70	49	41
72	35	43
72	40	43
72	42	43
73	45.5	44
74	42	45
74	49	45
76	49	47
77	52	48
77	57.5	48

Notes:

This species tends to synchronize calls with sounds broadcast in the field (Luquillo mountains, Caribbean National Forest, Puerto Rico, July, 1982).

The tone level is that required to produce a criterion degree of call-synchronization for each individual animal, and the noise level is that then required to reduce the tone-evoked synchronous calling response below some criterion amount. Noise was continuous, with an 800 Hz bandwidth at a center frequency of 1300 Hz. Tones were 100 msec bursts. N=17.

The correlation coefficient (r) is 0.63.

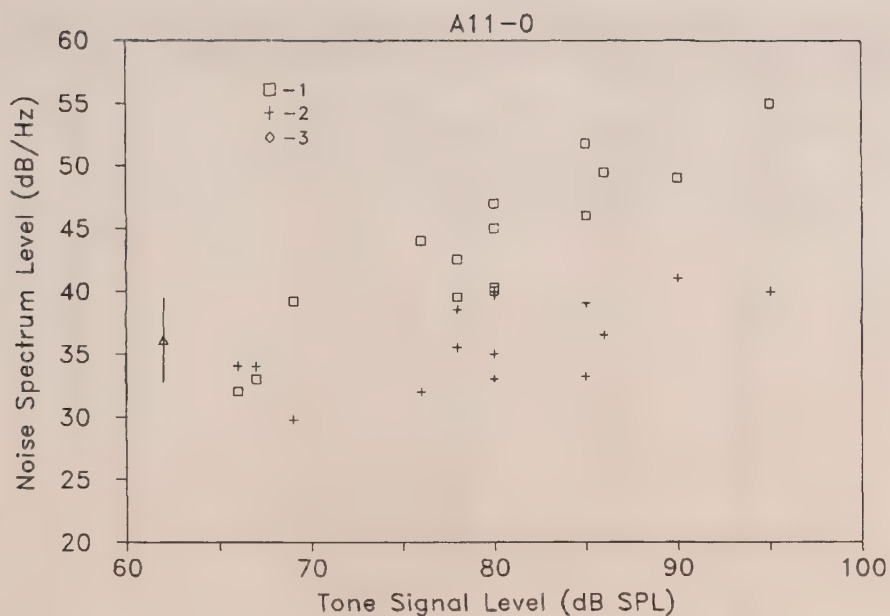


Fig. A11-0. Relation between the tone level required for a criterion degree of call suppression, and the noise level required to reduce this response, in *Eleutherodactylus coqui* (neotropical tree frog).

- 1- Noise level required to reduce response to zero
- 2- Signal-to-noise ratio for condition #1
- 3- Mean \pm 1sd of signal-to-noise ratio values of #2

Reference:

Narins, P.M. (1982) Effects of masking noise on evoked calling in the Puerto Rican coqui (Anura: Leptodactylidae). J. Comp. Physiol. 147, 439-446.

Table A11-0. Relation between the tone level required for a criterion degree of call suppression, and the noise level required to reduce this response, in *Eleutherodactylus coqui* (neotropical tree frog).

Stimulus Tone Level (dB SPL)	Noise Spectrum Level (dB/Hz)	Signal- to-noise Ratio (dB)
	1	2
66	32	34
67	33	34
69	39.2	29.8
76	44	32
78	42.5	35.5
78	39.5	38.5
80	40	40
80	40.3	39.7
80	45	35
80	47	33
85	46	39
85	51.8	33.2
86	49.5	36.5
90	49	41
95	55	40

Notes:

In field studies with this species, (Luquillo mountains, Puerto Rico, May and June, 1980), the broadcast of tone bursts caused the inhibition of the second note of the normal two-note "advertisement" call. In this experiment, 1 kHz tone bursts (5 msec rise/fall times) were presented from 0.2 to 0.6 times per sec. Signal level was raised until 20% of the calls were inhibited. Then, continuous broad band noise was introduced and noise level was increased until the inhibitory effects of the tone signals were eliminated. N=17.

The tone level required for a 20% inhibition of call suppression, minus the noise level required to reduce this response to zero is defined here as the effective critical masking ratio. The mean S/N plotted is 36.1 dB with a standard deviation of 3.33 dB.

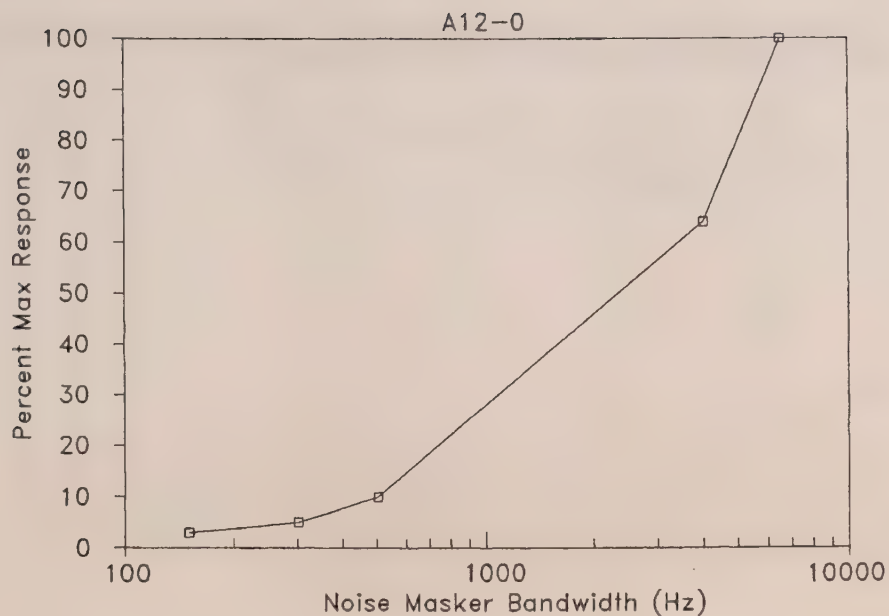


Fig. A12-0. The effect of masker bandwidth on the tone-evoked call suppression response in *Eleutherodactylus coqui* (neotropical tree frog).

Reference:

Narins, P.M. (1982) Effects of masking noise on evoked calling in the Puerto Rican coqui (Anura: Leptodactylidae). *J. Comp. Physiol.* 147, 439-446.

Table A12-0. The effect of masker bandwidth on the tone-evoked call suppression response in *Eleutherodactylus coqui* (neotropical tree frog).

Noise Bandwidth (Hz)	Percent Maximum Response
150	3
300	5
500	10
4000	64
6500	100

Notes:

See Notes for Fig. A11-0.

In this field experiment, an effective critical bandwidth was determined by assessing the effectiveness of a noise masker as a function of its bandwidth, with total noise power held constant. Noise was continuous, and the signal was a 1 kHz tone (as in Fig. A11-0) adjusted in amplitude to produce a 20% call suppression response. Using a threshold of 10% of maximum response, the effective critical bandwidth was determined to be 500 Hz at a center frequency of 1 kHz. N=13.

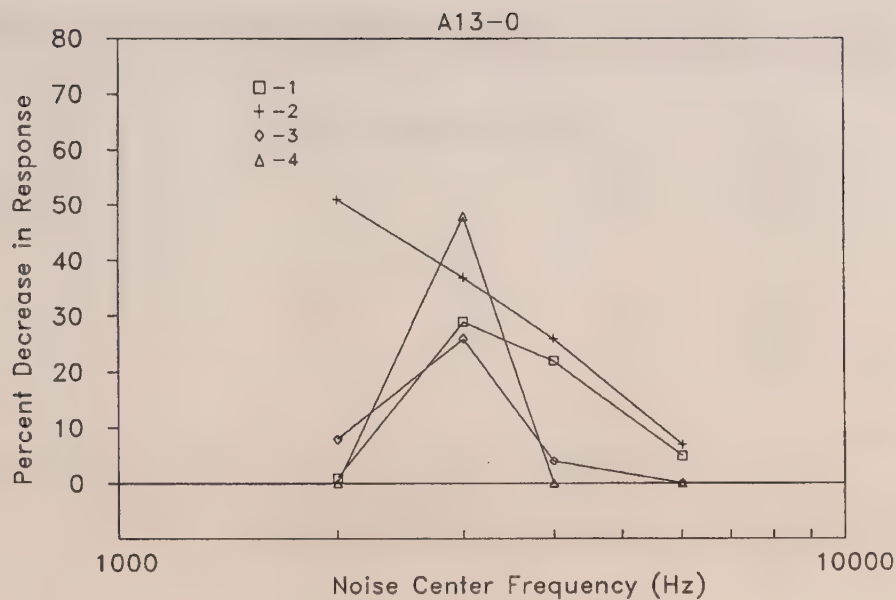


Fig. A13-0. The effect of background noise center frequency and level on calling rate in *Hyla ebraccata* (neotropical tree frog).

- 1- 90 dB, Percent decrease in number of calls
- 2- 100 dB, Percent decrease in number of calls
- 3- 90 dB, Decrease in percentage of multi-note calls
- 4- 100 dB, Decrease in percentage of multi-note calls

Reference:

Schwartz, J.J. & Wells, K.D. (1983) The influence of background noise on the behavior of a neotropical treefrog, *Hyla ebraccata*. *Herpetologica* 39, 121-129.

Table A13-0. The effect of background noise center frequency and level on calling rate in *Hyla ebraccata* (neotropical tree frog).

Noise Center Frequency (Hz)	Percent Decrease in Response			
	1	2	3	4
2000	1	51	8	0
3000	29	37	26	48
4000	22	26	4	0
6000	5	7	0	0

Notes:

Field experiments conducted in a flooded field, Gamboa, Panama, July and August, 1982. Noise was 1/3 octave bands centered at 2,3,4 and 6 kHz. Noise presented in 30 sec bursts separated by 30 sec of silence. Noise suppresses normal calling in these species, presumably by masking the sounds of nearby males. N=12 to 14 males.

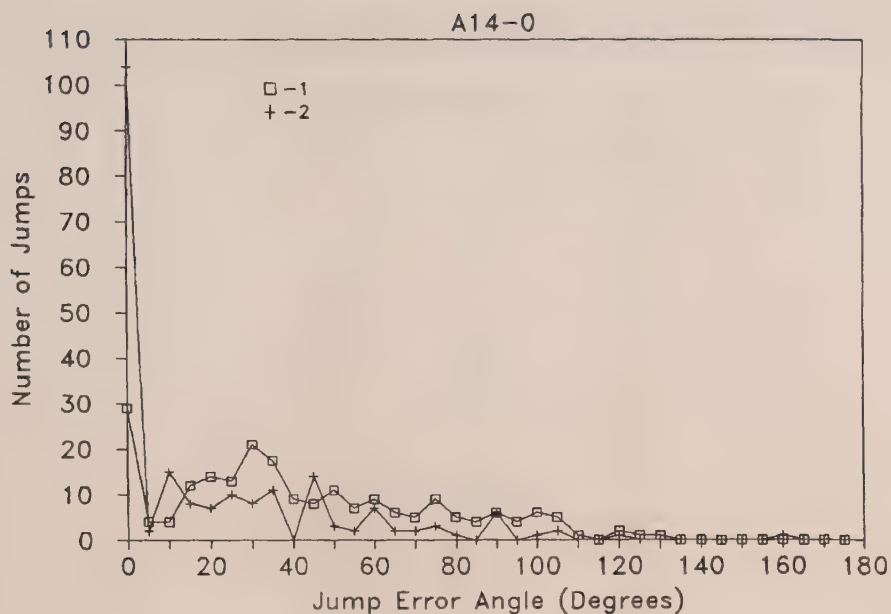


Fig. A14-0. Distributions of jump error angles in 2- and 3-dimensional approach to sound sources in *Hyperolius marmoratus* (painted reed frog).

1- 3-dimensional grid, mean=43 degrees
 2- 2-dimensional grid, mean=22 degrees

Reference:

Passmore, N.I., Capranica, R.R., Telford, S.R., & Bishop, P.J. (1984) Phonotaxis in the painted reed frog (*Hyperolius marmoratus*). *J. Comp. Physiol.* 154, 189-197.

Table A14-0. Distributions of jump error angles in 2- and 3-dimensional approach to sound sources in *Hyperolius marmoratus* (painted reed frog).

Jump Error Angle (Degrees)	Number of Jumps	
	1	2
0	29	104
5	4	2
10	4	15
15	12	8
20	14	7
25	13	10
30	21	8
35	17.5	11
40	9	0
45	8	14
50	11	3
55	7	2
60	9	7
65	6	2
70	5	2
75	9	3
80	5	1
85	4	0
90	6	6
95	4	0
100	6	1
105	5	2
110	1	0
115	0	0
120	2	1
125	1	0
130	1	0
180	0	1

Notes:

Female animals were observed approaching a sound source broadcasting the male mating call in a 3-dimensional (N=17) and 2-dimensional, horizontal grid (N=13). The angular error of each of the many jumps required to reach the sound source was recorded during each approach. These jump error angles are direct estimates of this species' capabilities for directional hearing.

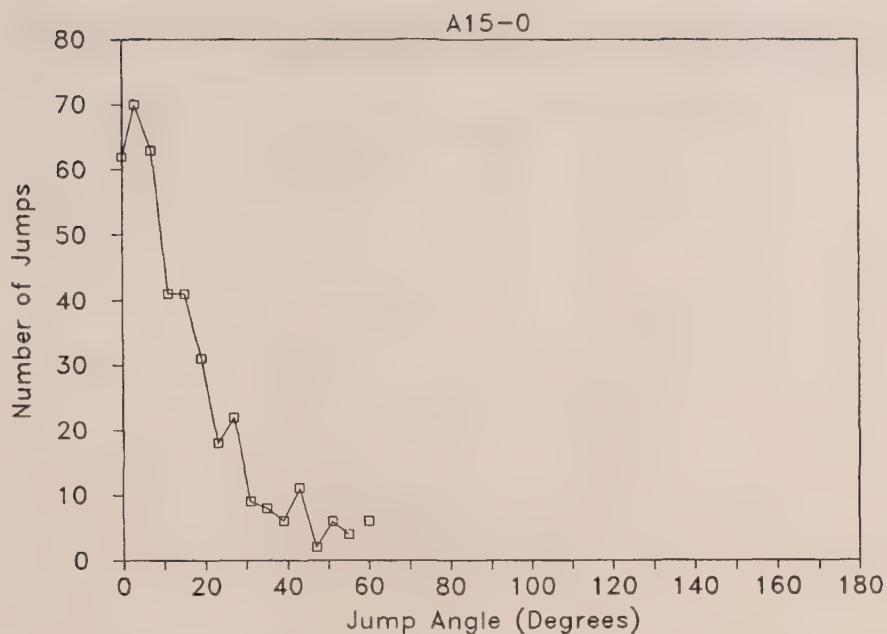


Fig. A15-0. Distribution of jump error angles by *Hyla cinerea* (green tree frog) approaching a sound source in 2-dimensions (horizontal plane).

Reference:

Rheinlaender, J., Gerhardt, H.C., Yager, D.D., and Capranica, R.R. (1979) Accuracy of phonotaxis by the Green Treefrog (*Hyla cinerea*). J. Comp Physiol. 133, 247-255.

Table A15-0. Distribution of jump error angles by *Hyla cinerea* (green tree frog) approaching a sound source in 2-dimensions (horizontal plane).

Jump Error Angle (Degrees)	Number of Jumps
0	62
3	70
7	63
11	41
15	41
19	31
23	18
27	22
31	9
35	8
39	6
43	11
47	2
51	6
55	4
60	6

Notes:

42 female frogs were observed in 156 approaches to a sound source broadcasting the equivalent of the male mating call. The arena was 3.75 meters long, and only jumps farther than 1 meter from the source were recorded. Mean jump angle is 16.1 degrees. Use of synthetic calls demonstrated that high frequency components in the 3 kHz region, normally a part of the mating call, do not enhance the accuracy of sound localization.

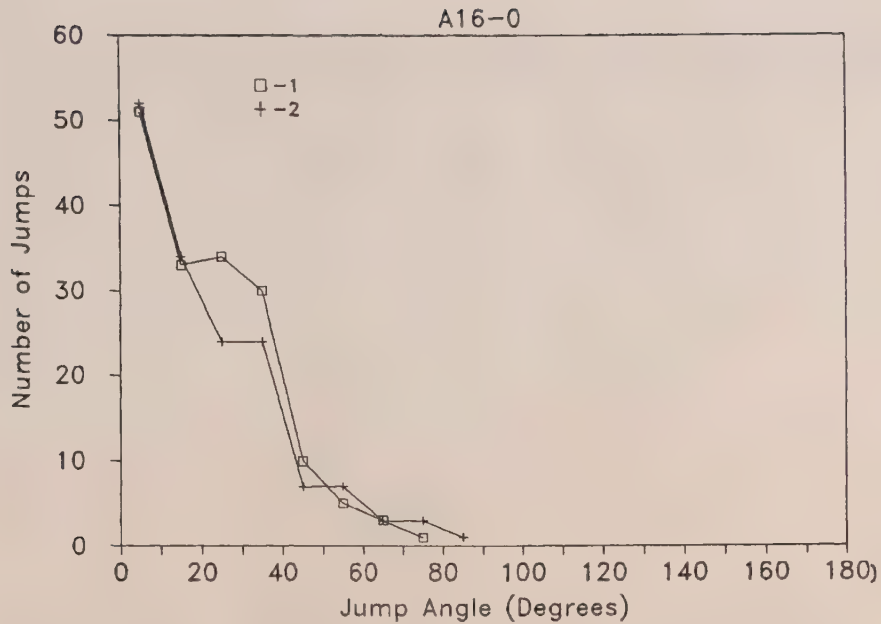


Fig. A16-0. Distribution of jump error angles in the horizontal plane for the dendrobatid frog, *Colostethus nubicola*, approaching a sound source broadcasting the male mating call.

- 1- Jumps to the right
- 2- Jumps to the left

Reference:

Gerhardt, H.C. & Rheinlaender, J. (1980) Accuracy of sound localization in a miniature dendrobatid frog. *Naturwissenschaften* 67, 362-363.

Table A16-0. Distribution of jump error angles in the horizontal plane for the dendrobatid frog, *Colostethus nubicola*, approaching a sound source broadcasting the male mating call.

Jump Error Angle (Degrees)	Number of Jumps	
	1	2
5	51	52
15	33	34
25	34	24
35	30	24
45	10	7
55	5	7
65	3	3
75	1	3
85		1

Notes:

In this experiment, a calling male was identified in this species' usual environment (lowland forests of Central America), and a grid system and loudspeaker introduced without disturbing the animal. A recording of a conspecific call was broadcast from the loudspeaker, and the male approached. This distribution of errors is for 22 approaching males, making a total of 324 jumps. Mean jump angle is 23 degrees.

This study illustrates good localization behavior in the noisy, natural environment. Interaural distance is about 5 mm for this species. The mating call has peak amplitude in the 5-6 kHz region. The authors calculate that this species must process an interaural temporal difference of 10 microsec, or less, under the assumption that interaural time differences are the cues used in localization.

Hearing in Birds

Interest in the hearing of birds has long been high because of the many and varied bird vocalizations that are so familiar to everyone. In fact, many of the psychophysical studies of bird hearing carried out over the past 40 years or so were motivated, at least in part, by observations that bird vocalizations contain complex temporal and spectral patterns and transitions, and that the birds themselves appear to be able to use this rather "densely packed" information for species recognition and individual recognition, as well as for communicating in a variety of social and agonistic situations. This suggested that birds may have particularly acute temporal and spectral discrimination capacities. The many psychophysical studies of bird hearing have confirmed that birds do, in fact, have good sensitivity in time and frequency analysis, and in localization abilities. However, as the data compiled in this section show, their abilities are not atypical of vertebrates in general. Another reason for the experimental interest in bird hearing is that some species are well known for their abilities to mimic human speech as well as the calls of other bird species. We have possibly implicitly assumed that this ability demonstrated clearly superior (i.e. humanoid) auditory abilities. As is shown throughout this volume, however, neither bird nor human hearing are clearly superior to those of many other vertebrates.

The outer ear of birds includes a feather-covered external canal, with no pinna as it is usually conceived. The feathers covering the external canals seem specially adapted for minimizing air turbulence (and thus noise) during flight. In some species such as the barn owl, the feathers surrounding the ears constitute the functional equivalent of a pinna, and have been described as a parabolic reflector for increasing the efficiency of sound transmission to the inner ear, and for gaining directional sensitivity. The external bony canals of the barn owl are bilaterally asymmetrical. This is an adaptation for increasing interaural cues, and thus localization abilities, in the vertical plane.

The bird middle ear is similar to those of the amphibians and reptiles in having a single major ossicle, the columella or stapes. The efficiency and frequency response of this system is not unlike that of mammals in the frequency range below about 2000 Hz. The columellar middle ear probably should not be considered the major factor limiting the frequency range of hearing since at least one species (the barn owl) has extended its range considerably without abandoning the columella design. It is likely that the limitation of frequency range among the birds (and the hearing range of most all vertebrates for that matter) is a specific adaptation for efficient sound processing, given the demands for sound processing and the central neural strategies for carrying it out.

The inner ear of birds includes a cochlea in addition to an associated lagena, and the vestibular saccule, utricle, and semi-circular canal cristae. The function of the lagena is not known, but may function in the detection of very low frequency sound. The cochlea is elongated and slightly "bent," similar to the auditory papillae of some reptiles (e.g. the caiman). A cross-section of the bird basilar membrane and papilla shows many rows of hair cells which vary in height across the membrane. There is as yet no clear evidence for a classification of inner and outer hair cells

as there is among mammals. In general, the height of the hair cell stereocilia varies smoothly from one end of the papilla to the other. Long stereocilia have been associated with low frequency sensitivity, and short cilia with high frequency sensitivity. It is likely that a frequency analysis occurs along the basilar membrane of the bird ear in much the same way that it occurs among mammals.

Audiograms for about 22 bird species show a best sensitivity from about -10 to 10 dB SPL in the frequency range between 1000 and 3000 Hz (Figs. B1-0 to B10-0), with the barn owl showing optimal sensitivity out to 6000 - 7000 Hz (Fig. B8-0). In the chicken, hearing develops from low frequencies to high in the first days of life (Fig. B9-0).

Optimal intensity discrimination thresholds (about 1 to 3 dB) are well within the range for fishes and mammals, are independent of frequency (Fig. B12-0), and in some cases show declining values at higher sound levels (Fig. B11-0), indicating a miss to Weber's Law.

Optimal frequency discrimination thresholds fall well within the mammalian range (from below 1% to about 10%) (Figs. B37-0 to B39-0). The lowest frequency discrimination thresholds for birds are about equal to those for the human. Frequency discrimination acuity increases with sound level at low frequencies, but deteriorates with sound level above 4000 Hz.

Different bird species show two different patterns of critical masking ratios (CR): A "standard" pattern in which the masked tone threshold increases about 3 dB per octave (Figs. B13-0), and a pattern showing flat or decreasing CRs up to 4000 to 5000 Hz (Fig. B14-0). In some species and at some frequencies, the CR declines with increasing masker level (Fig. B15-0). In general, masking is a nearly linear function of masker level (Figs B16-0 to B18-0). Birds show critical bands (CB) (Fig. B19-0), and CBs are about 2.5 times larger than CR bandwidths, as they are in humans Fig. B20-0).

Psychophysical tuning curves (PTC) and other estimates of auditory filters (Figs. B21-0 to B32-0) show a high degree of frequency selectivity (Fig. B33-0), and rather symmetrical filter shapes which are nearly independent of signal or masker levels. PTCs in forward masking are narrower than those determined in simultaneous masking (Figs. B33-0 and B31-0). Backward, and combined forward-backward masking have been demonstrated in birds (Fig. B32-0 and B45-0). Birds seem to perceive sound frequency along a monotonic, pitch-like dimension (Fig. B35-0). Intense noise exposure shows frequency-dependent effects consistent with the auditory filter estimates (Fig. B36-0).

Temporal summation at threshold tends to be linear with log duration, giving time constants greater than 200 msec (Fig. B41-0).

Repetition rate and temporal interval discrimination is constant at about 10% (Fig. B42-0). The TMTF is mammal-like with a time constant of 1.25 msec (Fig. B43-0). The two-click threshold ranges from about 2 to 6 msec (Fig. B44-0).

Auditory localization is acute (MAA from about 2 to 20 degrees), with lowest thresholds for the barn owl (Figs. B47-0 to B56-0).

Loudness and pitch scaling methods have been applied successfully in some species (Figs. B57-0 to B59-0), and labeling of human speech phonemes has been demonstrated (Fig. B60-0).

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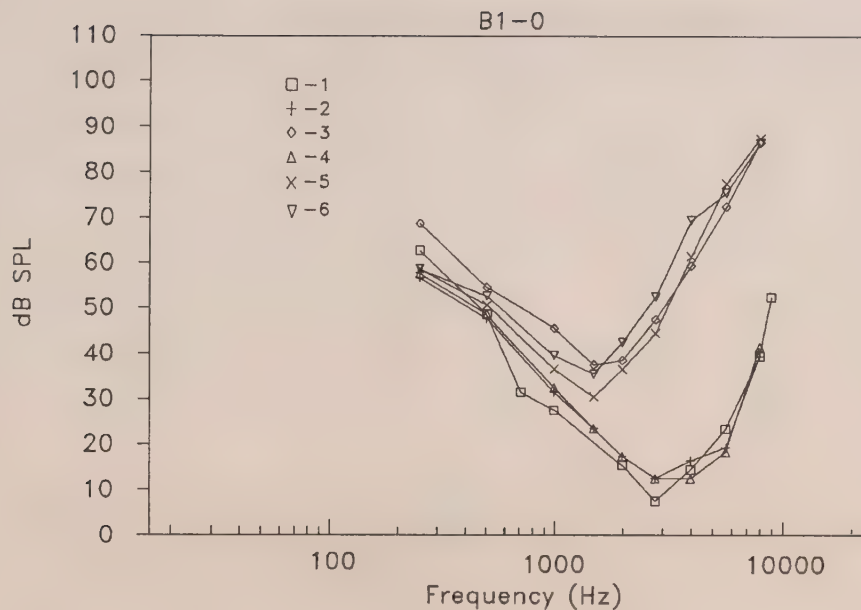


Fig. B1-0. Audiograms for the canary (*Serinus canarius*).

- 1- Dooling, Mulligan, and Miller, 1971 (Belgian waterschlager)
- 2- Okanoya and Dooling, 1987a (German roller)
- 3- Okanoya and Dooling, 1985 (Belgian waterschlager, Millbrook colony)
- 4- Okanoya and Dooling, 1985 (German roller and American singer)
- 5- Okanoya and Dooling, 1987b (Belgian waterschlager, Millbrook colony)
- 6- Okanoya and Dooling, 1987b (Belgian waterschlager, Greenspon colony)

References:

- Dooling, R.J., Mulligan, J.A., and Miller, J.D. (1971) Auditory sensitivity and song spectrum of the common canary (*Serinus canarius*). *J. Acoust. Soc. Amer.* 50, 700-709.
- Okanoya, K., and Dooling, R.J. (1985) Colony differences in auditory thresholds in the canary. *J. Acoust. Soc. Amer.* 78, 1170-1176.
- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Okanoya, K., and Dooling, R.J. (1987b) Strain differences in auditory thresholds in the canary (*Serinus canarius*). *J. Comp. Psychol.* 101, 213-215.

Table B1-0. Audiograms for the canary (*Serinus canarius*).

Frequency (Hz)	Sound Pressure (dB SPL)					
	1	2	3	4	5	6
250	63	57	69	58	59	59
500	49	48	55	49	51	53
710	32					
1000	28	32	46	33	37	40
1500		24	38	24	31	36
2000	16	18	39	18	37	43
2800	8	13	48	13	45	53
4000	15	17	60	13	62	70
5700	24	20	73	19	78	76
8000	40	40	87	42	88	87
9000	53					

Notes:

1- Instrumental shock avoidance conditioning in a shuttle box using a staircase-like psychophysical procedure. N=4, 2 male and 2 female, between 9 and 26 months old.

2- Operant conditioning for food reward using the staircase psychophysical procedure. Animals were trained to peck one key (observation key) repeatedly when a tone was absent, and to switch responses to another key when a tone was present. One male animal.

3- Same procedure as #2. Adult Belgian waterschlager canaries from the colony maintained at Millbrook, NY (Rockefeller University field research station). Canaries from this colony have been used extensively in studies of vocal learning (e.g. Nottebohm, 1980). These data show poor high frequency hearing for the Millbrook colony (50 dB less sensitive at 6 kHz than the other canaries tested). One male, four females, 26-76 months old.

4- Same procedure as #2. Median of three German rollers and one American singer. Since the data for other Belgian waterschlagers tested earlier (Dooling, Mulligan, and Miller, 1971) show sensitivity similar to these other strains, the authors concluded that the hearing sensitivity difference may be a colony difference.

5-6- Same procedure as #2. In this experiment, Belgian waterschlagers from the Millbrook (N=5) and Greenspon (N=2) colonies were compared with each other, and with non-waterschlagers (N=2).

5- Data for the Millbrook colony animals (juveniles). The Millbrook canaries showed hearing levels essentially similar to those tested earlier (#3 above). The non-waterschlagers showed hearing levels essentially like those in #1, #2, and #4 above.

6- Data for the Greenspon colony of Belgian waterschlagers. The fact that waterschlagers from two different colonies show poor high frequency hearing suggests that this is a strain difference in hearing, and not a colony difference as suggested by Okanoya and Dooling (1985). The authors suggest that the waterschlagers studied by Dooling, Mulligan, and Miller (1971) (#1) may not have been pure bred.

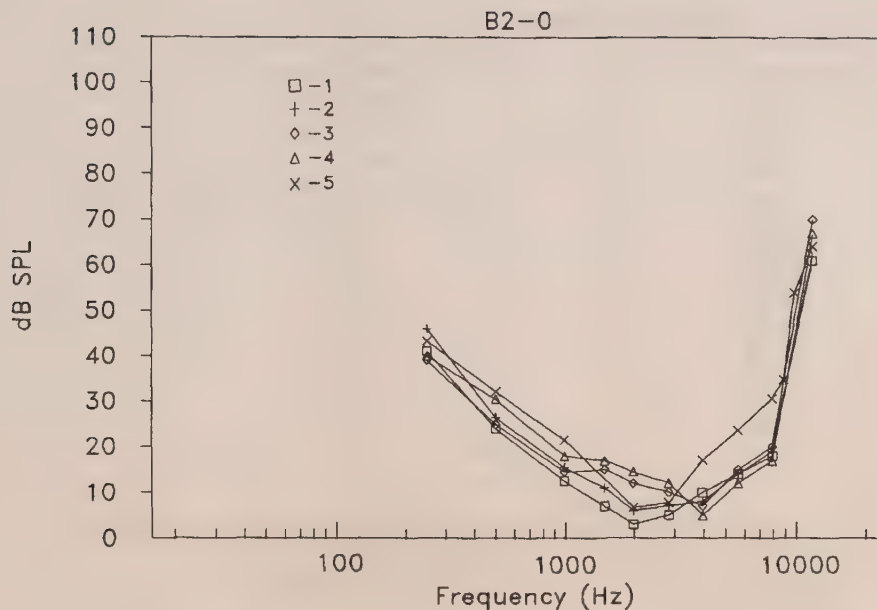


Fig. B2-0. Audiograms for sparrows.

- 1- *Melospiza melodia* - song sparrow (Okanoya and Dooling, 1987a)
- 2- *Melospiza georgiana* - swamp sparrow (Okanoya and Dooling, 1987a)
- 3- *Melospiza melodia* - song sparrow (Okanoya and Dooling, 1988)
- 4- *Melospiza georgiana* - swamp sparrow (Okanoya and Dooling, 1988)
- 5- *Spizella pusilla* - field sparrow (Dooling, Peters and Searcy, 1979)

References:

- Dooling, R.J., Peters, S., and Searcy, M.H. (1979) Auditory sensitivity and vocalizations of the field sparrow (*Spizella pusilla*). *Bull. Psychonom. Soc.* 14, 106-108.
- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Okanoya, K., and Dooling, R.J. (1988) Hearing in the swamp sparrow (*Melospiza georgiana*) and the song sparrow (*Melospiza melodia*). *Anim. Behav.* 36 (in press).

Table B2-0. Audiograms for sparrows.

Frequency (Hz)	Sound Pressure (dB SPL)				
	1	2	3	4	5
250	41	46	39	40	43.3
500	24	26.5	25	30.5	32.2
1000	12.5	15.5	14.5	18	21.5
1500	7	11	15	17	
2000	3	6	12	14.5	6.67
2860	5	7	10	12	7.75
4000	10	8	7	5	17.1
5700	14	14	15	12	23.6
8000	18	19	20	17	30.6
9000					34.9
10000					53.9
12000	61	62	70	67	64.1

Notes:

- 1-2- Operant conditioning with food reward using the staircase psychophysical procedure. See Notes for Fig. B1-0. One male animal.
- 3- Same procedures as #1 and #2. Two males and one female.
- 4- Same procedures as #1 and #2. Two males.
- 5- Instrumental shock avoidance conditioning using a modified method of limits psychophysical procedure. Restrained animals were trained to bite a bar during tone presentations in order to avoid shock. Sound pressure level could be specified at the bird's head. Two males.

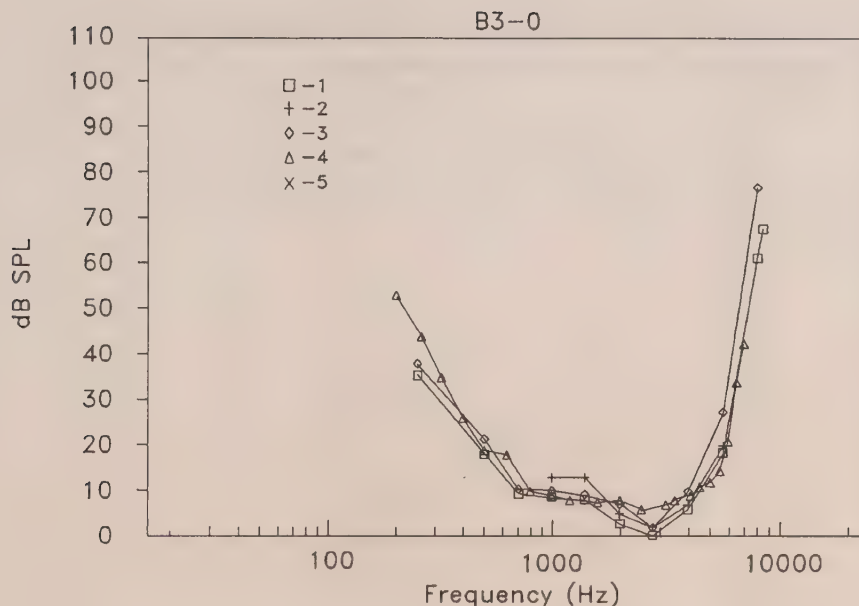


Fig. B3-0. Audiograms for *Melopsittacus undulatus* (budgerigar or parakeet).

- 1- Dooling and Saunders, 1975
- 2- Saunders and Dooling, 1974
- 3- Okanoya and Dooling, 1987a
- 4- Saunders and Pallone, 1980
- 5- Saunders, Rintelmann, and Bock, 1979

References:

- Dooling, R.J., and Saunders, J.C. (1975) Hearing in the parakeet (*Melopsittacus undulatus*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations. *J. Comp. Physiol. Psychol.* 88, 1-20.
- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Saunders, J., and Dooling, R.J. (1974) Noise-induced threshold shift in the parakeet (*Melopsittacus undulatus*). *Proc. Nat. Acad. Sci. USA* 71, 1962-1965.
- Saunders, J., and Pallone, R. (1980) Frequency selectivity in the parakeet studied by isointensity masking contours. *J. Exp. Biol.* 87, 331-342.
- Saunders, J., Rintelmann, W., and Bock, G. (1979) Frequency selectivity in bird and man: A comparison among critical ratios, critical bands and psychophysical tuning curves. *Hear. Res.* 1, 303-323.

Table B3-0. Audiograms for *Melopsittacus undulatus* (budgerigar or parakeet).

Frequency (Hz)	Sound Pressure (dB SPL)				
	1	2	3	4	5
200				53	47
250	35.5		38		35
260				44	
315					29
320				35	
400				26	24.5
500	18.1		21.5	19	
630				18	15
710	9.4		10.5		
800				10	12
1000	8.7	13	10.2	9	9.7
1200				8	
1250					9.7
1400	8.2	13	9.3		
1600				7.5	8
2000	2.8	5	7.1	8	7.5
2500				6	3
2800	0.25	2	2		
3000					3.5
3200				7	
3500				8	6
4000	6	7	10		8.5
4100				9	
4500				11	
5000				12	12.5
5500				14.5	
5700	18.5	20	27.5		
6000				21	23
6500				34	
7000				42.5	42.5
8000	61.4		77		61
8500	67.8				68

Notes:

1- Instrumental shock avoidance conditioning using the method of limits psychophysical procedure. A restrained bird was trained to bite a rod upon the presentation of a tone in order to avoid shock. Means: N=4 (2 males, 2 females) 6-16 weeks old.

2- Same procedures as #1. Means: N=4 16-week-old birds, surgically deafened in the left ear.

3- Operant conditioning for a food reward using the staircase psychophysical procedure. See Notes for this reference in Fig. B1-0. Means: N=2 males.

4- Same procedures as #1. Means: N=4.

5- Same procedures as #1. Means: N=6.

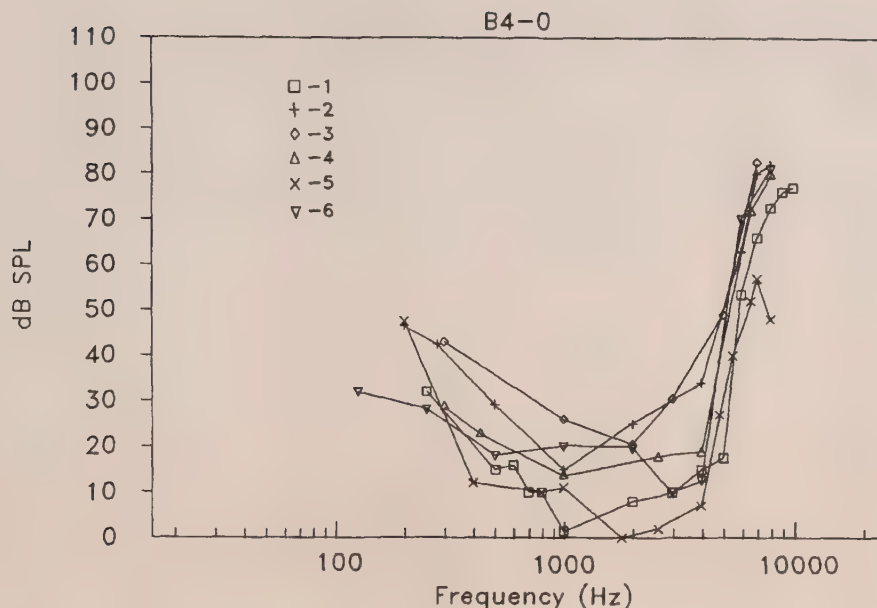


Fig. B4-0. Audiograms for the pigeon (*Columba livia*).

- 1- Goerdel-Leich and Schwartzkopff, 1984
- 2- Stebbins, 1970
- 3- Trainer, 1946
- 4- Heise, 1953
- 5- Harrison and Furumoto, 1971
- 6- Hienz, Sinnott, and Sachs, 1977

References:

- Goerdel-Leich, A., and Schwartzkopff, J. (1984) The auditory threshold of the pigeon (*Columba livia*) by heart-rate conditioning. *Naturwissenschaften* 71, S. 98.
- Harrison, J.B., and Furumoto, L. (1971) Pigeon audiograms: Comparison of evoked potential and behavioral thresholds in individual birds. *J. Aud. Res.* 11, 33-42.
- Hienz, R.D., Sinnott, J.M., and Sachs, M.B. (1977) Auditory sensitivity of the red-winged blackbird (*Agelaius phoeniceus*), and brown-headed cowbird (*Molothrus ater*). *J. Comp. Physiol. Psychol.* 91, 1365-1376.
- Heise, G.A. (1953) Auditory thresholds in the pigeon. *Am. J. Psychol.* 66, 1-19.
- Stebbins, W. (1970) Studies of hearing and hearing loss in the monkey. In W.C. Stebbins (ed), *Animal Psychophysics: The Design and Conduct of Sensory Experiments*. New York: Appleton-Century-Crofts.
- Trainer, J.E. (1946) The auditory acuity of certain birds. Unpublished Doctoral Dissertation, Cornell University.

Table B4-0. Audiograms for the pigeon (*Columba livia*).

Frequency (Hz)	Sound Pressure (dB SPL)					
	1	2	3	4	5	6
125						32
200		48			47.5	
250	32					28
280		42.5				
300			43	29		
400					12	
430				23		
500	15	29.2				18
600	16					
700	10					
800	10				10	
1000	1.5	15	26	14	11	20
1800					0	
2000	8	27	20.5			19.5
2600				18	2	
3000	9.8		30.5			10
4000	15	34		19	7	12.5
4800					27	
5000	17.5		49			
5600					40	
6000	53.5	63				70
6600				72	52	
7000	66	80	82.5		57	
8000	72.5	86		80	48	81
9000	76					
10000	77					

Notes:

1- Classical conditioning of heart rate using the method of constant stimuli.

Medians: N=3.

2- Operant conditioning for a food reward using the staircase psychophysical procedure. Means: N=2.

3- Instrumental shock avoidance with a non-specific motor response using the descending method of limits. Median of one white female, one black female, and a black-and-white male.

4- Operant conditioning for a food reward using the modified method of limits. The threshold at each frequency represents averaged data from one to five animals.

5- Operant conditioning for a food reward using a modified method of constant stimuli. Animals trained to peck a key in the presence of a continuous pure tone (VI schedule), and extinguished in quiet. Means: N=6 male white Carneaux pigeons.

6- Operant conditioning for a food reward (go, no-go procedure) using the method of constant stimuli. Means: N=2 male white Carneaux pigeons.

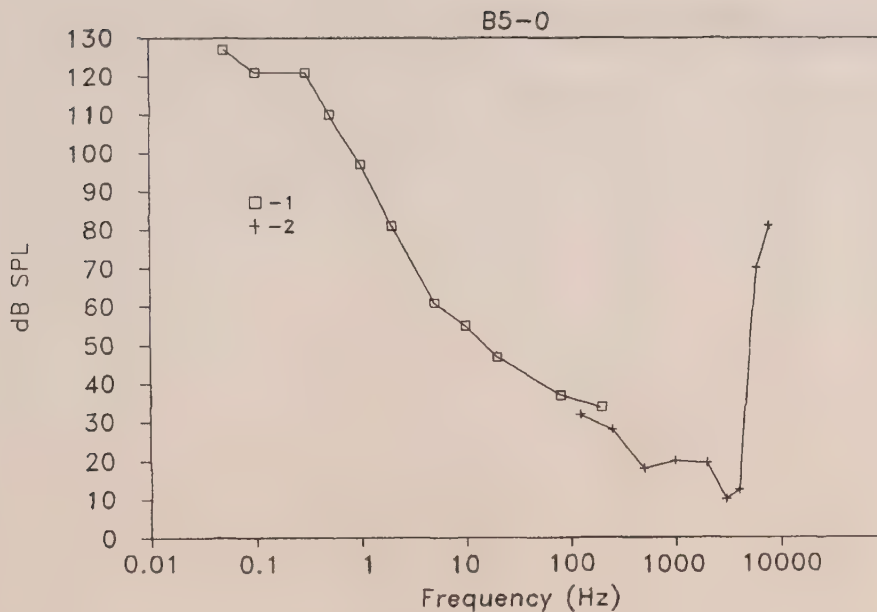


Fig. B5-0. Audiogram for the pigeon (*Columba livia*) at "audio" and "infrasonic" (very low) frequencies.

- 1- Kreithen and Quine (1979) "infrasound" audiogram
- 2- Hienz, Sinnott, and Sachs (1977) (representative "audio" frequency sensitivity)

References:

- Hienz, R.D., Sinnott, J.M., and Sachs, M.B. (1977) Auditory sensitivity of the red-winged blackbird (*Agelaius phoeniceus*), and brown-headed cowbird (*Molothrus ater*). J. Comp. Physiol. Psychol. 91, 1365-1376.
- Kreithen, M.L., and Quine, D.B. (1979) Infrasound detection by the homing pigeon: A behavioral audiogram. J. Comp. Physiol. 129, 1-4.

Table B5-0. Audiogram for the pigeon (*Columba livia*) at "audio" and "infrasonic" (very low) frequencies.

Frequency (Hz)	Sound Pressure (dB SPL)	
	1	2
0.05	127	
0.1	121	
0.3	121	
0.5	110	
1	97	
2	81	
5	61	
10	55	
20	47	
80	37	
125		32
200	34	
250		28
500		18
1000		20
2000		19.5
3000		10
4000		12.5
6000		70
8000		81

Notes:

1- Two loudspeakers operated into a sealed chamber containing the bird. These operated in phase (both raising and then lowering the pressure in the box) to produce sound pressure fluctuations as low as 0.05 Hz. When these were operated in a push-pull manner (one raising the pressure and the other lowering the pressure in the box), no net pressure change occurred. This served as a control condition for spurious speaker noises.

Classical cardiac conditioning (bradycardia) with shock as the UCS using a type of adaptive tracking psychophysics. Five Cornell homing pigeons.

2- Operant conditioning for a food reward (go, no-go procedure) using the method of constant stimuli. Two male white Carneaux pigeons. Same data as in Fig. B4-0, #6.

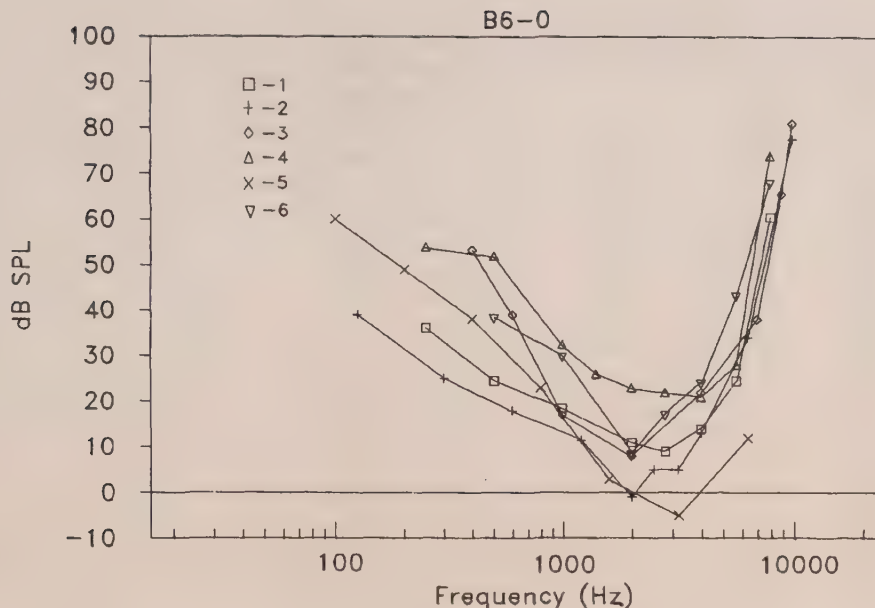


Fig. B6-0. Audiograms for the starling and three finches.

- 1- *Sturnus vulgaris* - starling (Dooling, Okanoya, Downing, and Hulse, 1986)
- 2- *Sturnus vulgaris* - starling (Kuhn, Muller, Leppelsack, and Schwartzkopff, 1982)
- 3- *Sturnus vulgaris* - starling (Trainer, 1946)
- 4- *Taeniofigia guttata* - zebra finch (Okanoya and Dooling, 1987a)
- 5- *Pyrrhula pyrrhula* - bullfinch (Schwartzkopff, 1949)
- 6- *Carpodacus mexicanus* - house finch (Dooling, Zoloth, and Baylis, 1978)

References:

- Dooling, R.J., Okanoya, K., Downing, J., and Hulse, S. (1986) Hearing in the starling (*Sturnus vulgaris*): Absolute thresholds and critical ratios. *Bull. Psychonom. Soc.* 24, 462-464.
- Dooling, R.J., Zoloth, S.R., and Baylis, J.R. (1978) Auditory sensitivity, equal loudness, temporal resolving power, and vocalizations in the house finch *Carpodacus mexicanus*. *J. Comp. Physiol. Psychol.* 92, 867-876.
- Kuhn, A., Muller, C.M., Leppelsack, H.-J., and Schwartzkopff, J. (1982) Heart rate conditioning used for determination of auditory thresholds in the starling. *Naturwissenschaften* 69, 245-246.
- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Schwartzkopff, J. (1949) Über Sitz und Leistung von Gehör und Vibrationssinn bei Vögeln. *Z. vergl. Physiol.* 31, 527-603.
- Trainer, J.E. (1946) The auditory acuity of certain birds. Unpublished Doctoral Dissertation, Cornell University.

Table B6-0. Audiograms for the starling and three finches.

Frequency (Hz)	Sound Pressure (dB SPL)					
	1	2	3	4	5	6
100					60.1	
125		39				
200					48.5	
250	36.2			54		
300		25				
400			53.2		38.3	
500	24.5			52		38.2
600		18	39			
800					23	
1000	18.5		17	32.5		29.6
1200		11.5				
1400				26		
1600					2.2	
2000	11	-1	8	23		8.2
2500		5				
2800	9			22		16.9
3200		5			-4.9	
4000	14	13	22	21		23.9
5700	24.5			28		43
6400		34			11.3	
7000			38			
8000	60.5			74		67.8
9000			65.5			
10000		77.5	81			

Notes:

- 1- Operant conditioning for a food reward using an adaptive tracking psychophysical procedure. N=1 male.
- 2- Classical cardiac conditioning with shock as the UCS, using the method of constant stimuli. N=7, but not all tested at each testing frequency.
- 3- Instrumental shock avoidance by a non-specific motor response. Medians: N=6. Not all birds tested at all frequencies.
- 4- Operant conditioning for a food reward using an adaptive tracking psychophysical procedure. N=1 male.
- 5- Operant conditioning for a food reward. Means: N=4.
- 6- Instrumental shock avoidance using a modified method of limits. Restrained animals trained to bite a bar to avoid shock. Means: N=4.

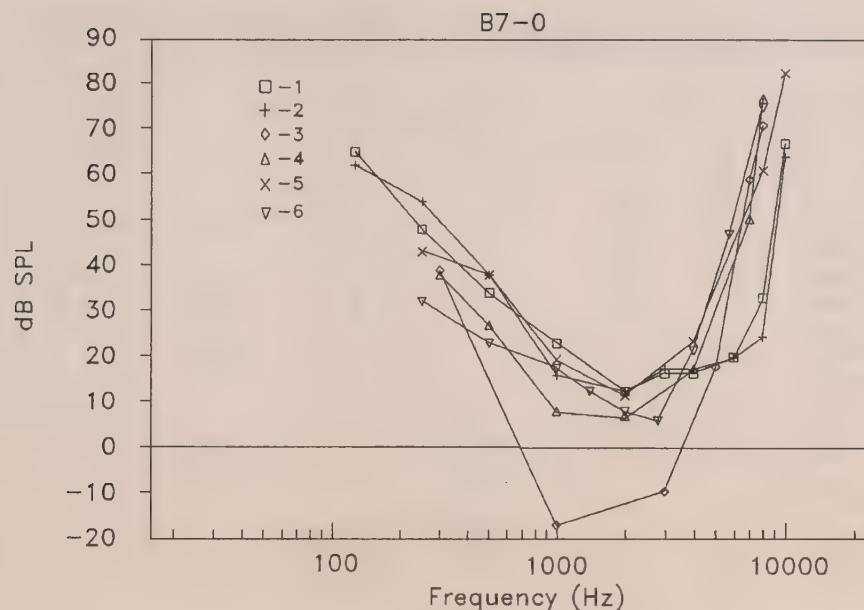


Fig. B7-0. Audiograms for six bird species (redwing blackbird, cowbird, crow, sparrowhawk, bluejay, and cockatiel).

- 1- *Agelaius phoeniceus* - redwing blackbird (Hienz, Sinnott, and Sachs, 1977)
- 2- *Molothrus ater* - brown-headed cowbird (Hienz, Sinnott, and Sachs, 1977)
- 3- *Corvus sp.* - crow (Trainer, 1946)
- 4- *Falco sparverius* - sparrowhawk (Trainer, 1946)
- 5- *Cyanocitta cristata* - bluejay (Cohen, Stebbins, and Moody, 1978)
- 6- *Nymphicus hollandicus* - cockatiel (Okanoya and Dooling, 1987a)

References:

- Cohen, S.M., Stebbins, W.C., and Moody, D.B. (1978) Audibility thresholds of the blue jay. *The Auk* 95, 563-568.
- Hienz, R.D., Sinnott, J.M., and Sachs, M.B. (1977) Auditory sensitivity of the red-winged blackbird (*Agelaius phoeniceus*), and brown-headed cowbird (*Molothrus ater*). *J. Comp. Physiol. Psychol.* 91, 1365-1376.
- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Trainer, J.E. (1946) The auditory acuity of certain birds. Unpublished Doctoral Dissertation, Cornell University.

Table B7-0. Audiograms for six bird species (redwing blackbird, cowbird, crow, sparrowhawk, bluejay, and cockatiel).

Frequency (Hz)	Sound Pressure (dB SPL)					
	1	2	3	4	5	6
125	65	62				
250	48	54			43	32
300			39	38		
500	34	38		27	38	23
1000	23	16	-17	8	19.5	17.5
1400						12.5
2000	12.5	12.5		7	11.5	8
2800						6
3000	16.5	17.5	-9.5			
4000	16.5	17.5		17.5	23.5	21.5
5700						47
5000			18			
6000	20	20				
7000			59	50.5		
8000	33	24.5	71	77	61	75
10000	67	64			82.5	

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli. Both a go, no-go procedure and a go-left, go-right procedure were used, and no significant differences were found. Means: N=10.

2- Same as #1. Means: N=6.

3- Instrumental shock avoidance by a non-specific motor response using the descending method of limits. N=1.

4- Same as #3. N=1.

5- Operant conditioning for a food reward using the method of constant stimuli. Means: N=2.

6- Operant conditioning for food reward using the staircase psychophysical procedure. Animals were trained to peck one key (observation key) repeatedly when a tone was absent, and to switch responses to another key when a tone was present. N=1.

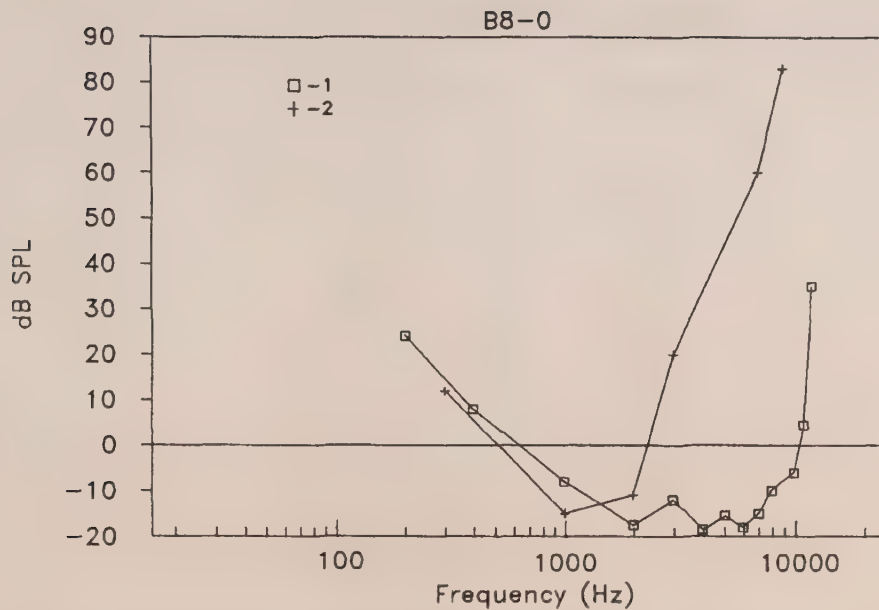


Fig. B8-0. Audiograms for two owl species (barn owl and great horned owl).

- 1- *Tyto alba* - barn owl (Konishi, 1973)
- 2- *Bubo virginianus* - great horned owl (Trainer, 1946)

References:

- Konishi, M. (1973) How the owl tracks its prey. *American Scientist* 61, 414-424.
- Trainer, J.E. (1946) The auditory acuity of certain birds. Unpublished Doctoral Dissertation, Cornell University.

Table B8-0. Audiograms for two owl species (barn owl and great horned owl).

Frequency (Hz)	Sound Pressure (dB SPL)	
	1	2
200	24	
300		12
400	8	
1000	-8	-15
2000	-17.5	-11
3000	-12	20
4000	-18.5	
5000	-15.5	
6000	-18	
7000	-15	60
8000	-10	
9000		83
10000	-6	
11000	4.5	
12000	35	

Notes:

1- Animals trained to take off from a perch for food reward upon presentation of a tone. Three animals were tested, but data were presented only for the "...most carefully tested" owl.

2- Instrumental shock avoidance by a non-specific motor response using the descending method of limits. N=1.

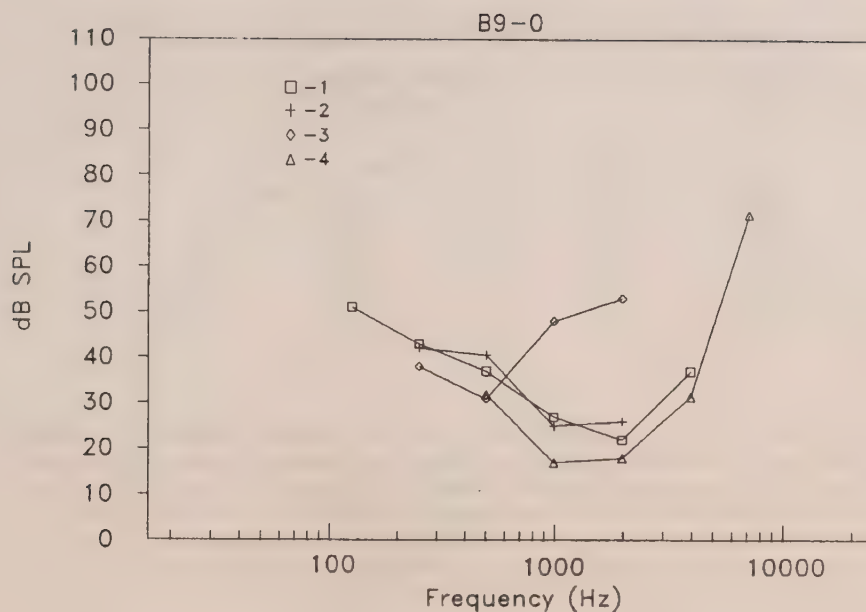


Fig. B9-0. Audiograms for the chicken at two ages, and for the turkey.

- 1- *Gallus gallus* (chicken, 4-day old), Gray and Rubel, 1985
- 2- *Gallus gallus* (chicken, 4-day old), Gray and Rubel, 1985
- 3- *Gallus gallus* (chicken, 0-day old), Gray and Rubel, 1985
- 4- *Meleagris gallopavo domesticus* (domestic turkey), Maiorana and Schleidt, 1972.

References:

- Gray, L., and Rubel, E.W. (1985) The development of absolute thresholds in chickens. *J. Acoust. Soc. Amer.* 77, 1162- 1172.
- Maiorana, V.A., and Schleidt, W.M. (1972) The auditory sensitivity of the turkey. *J. Aud. Res.* 12, 203-207.

Table B9-0. Audiograms for the chicken at two ages, and for the turkey.

Frequency (Hz)	Sound Pressure (dB SPL)			
	1	2	3	4
125	51			
250	43	42	38	
500	37	40.5	31	32
1000	27	25	48	17
2000	22	26	53	18
4000	37			31.5
7200				71.5

Notes:

1-3- The method of "peep suppression" was used in these studies on the chicken. This makes use of the tendency for young birds to peep incessantly when isolated, and the tendency for a novel sound stimulus to lengthen the interval between the first peep occurring during the sound, and the next peep. The length of this interval is defined as the degree of peep suppression. In an adaptive tracking procedure, the peep interval occurring during sound presentation is compared with the interval on control blank trials. A longer-than-usual interval is scored as a "yes", and an equal or shorter interval is scored a "no".

In this study, 0-day old chickens are tested on the day of hatching. The 4-day old chicks are considered nearly adult. Different groups of chickens are tested at each level of the independent variable (tone frequency).

1- 4-day old chicks, "yes-no" version of the tracking method. N=10 at each frequency tested.

2- 4-day old chicks, "forced choice" tracking method. N=80, 10 birds in each group.

3- 0-day old chicks, N=80, tested identically to #2

4- Classically conditioned suppression of an ongoing, food-reinforced operant response using a modified descending method of limits psychophysical procedure. Two adult females. These are averaged data from the three curves of Fig. B10-0, #1,2,3.

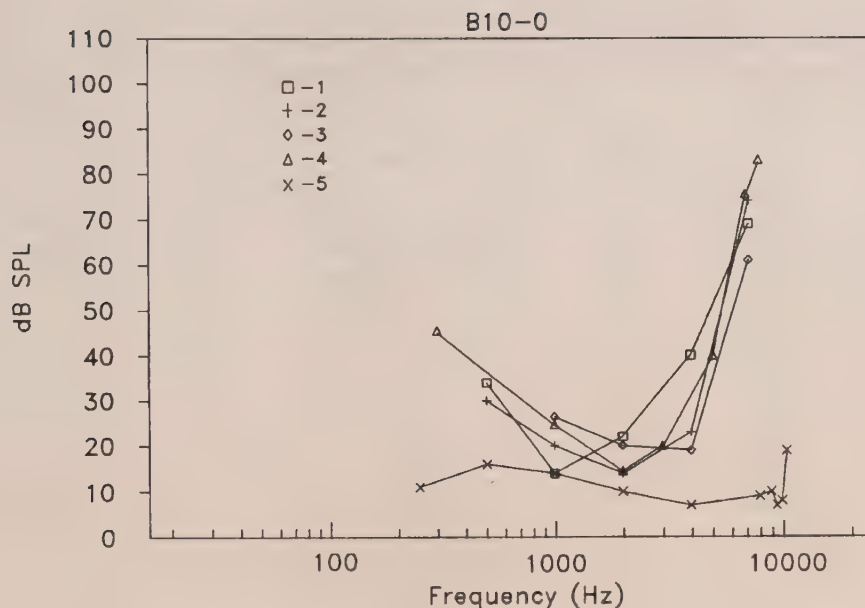


Fig. B10-0. Audiograms for the turkey, pheasant, and mallard duck.

1-3- *Meleagris gallopavo domesticus* - domestic turkey (Maiorana and Schleidt, 1972)

1- Hen #3; continuous tones

2- Hen #68; continuous tones

3- Hen #68; pulsed tones

4- *Anas platyrhynchos* - mallard duck (Trainer, 1946)

5- *Phasianus colchicus* - ring-necked pheasant (Stewart, 1955)

References:

Maiorana, V.A., and Schleidt, W.M. (1972) The auditory sensitivity of the turkey. *J. Aud. Res.* 12, 203-207.

Stewart, P.A. (1955) An audibility curve for two ring-necked pheasants. *Ohio J. Sci.* 55, 122-125.

Trainer, J.E. (1946) The auditory acuity of certain birds. Unpublished Doctoral Dissertation, Cornell University.

Table B10-0. Audiograms for the turkey, pheasant, and mallard duck.

Frequency (Hz)	Sound Pressure (dB SPL)*				
	1	2	3	4	5
300				45.5	
250					11
500	34	30			16
1000	14	20	26.5	24.7	14
2000	22	14	20	14.5	10
3000				20	
4000	40	23	19		7
5000				40	
7000				75.5	
7200	69	74	61		
8000				83	9
9000					10
9500					7
10000					8
10500					19

Notes:

* - See Note for #5.

1-3- Classically conditioned suppression of an ongoing, food-reinforced operant response using a modified descending method of limits psychophysical procedure. These are the individual data comprising the mean audiogram plotted in Fig. B8-0.

1- Hen #3, 5 sec continuous tones.

2- Hen #68, 5 sec continuous tones.

3- Hen #68, 5 sec of 200 msec on and 120 msec off pulsed tones.

4- Instrumental shock avoidance with a non-specific motor response using the descending method of limits. Means: N=2.

5- Note that sound pressure is given in dB "...above background level...". Instrumental shock avoidance ("...A reasonably vigorous jump within 10 seconds of the tone...") using a method of constant stimuli. These data are variable and not particularly stable (e.g. statistical significance of responses are not monotonic with stimulus intensity). These data are likely not valid absolute thresholds. Means: N=2.

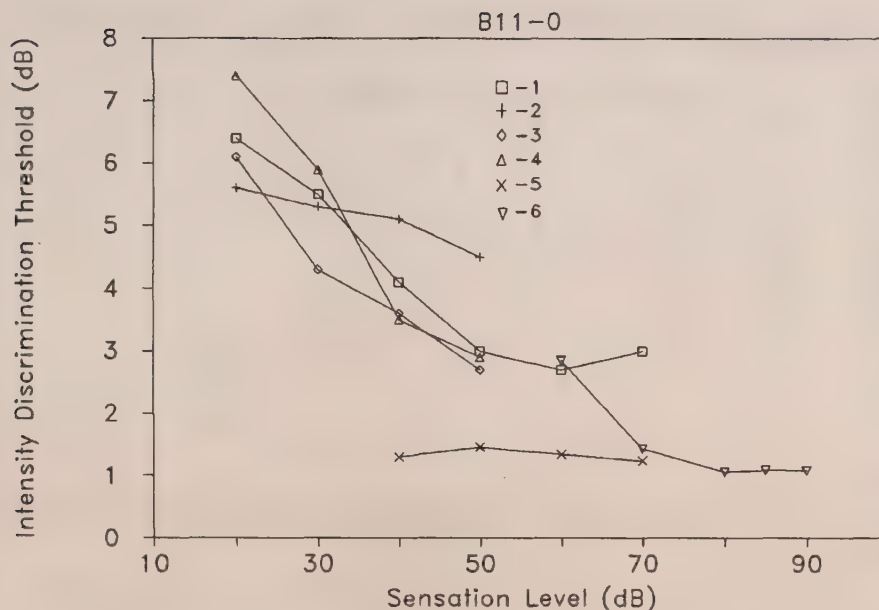


Fig. B11-0. Intensity discrimination thresholds as a function of sound intensity in several bird species.

- 1- *Melopsittacus undulatus* - parakeet (Dooling and Saunders, 1975)
- 2- *Agelaius phoeniceus* - redwing blackbird
Molothrus ater - brown headed cowbird
Columba livia - pigeon
 Data for 500 Hz signal averaged across these species.
- 3- Same as #2, 1000 Hz signal
- 4- Same as #2, 2000 Hz signal
 (Hienz, Sinnott, and Sachs, 1980)
- 5- *Melopsittacus undulatus* - parakeet (Dooling and Searcy, 1981) noise signal
- 6- *Serinus canarius* - canary, Belgian waterschlager, Millbrook colony, noise signal
 (Okanoya and Dooling, 1985)

References:

- Dooling, R.J., and Saunders, J.C. (1975) Auditory intensity discrimination in the parakeet (*Melopsittacus undulatus*). J. Acoust. Soc. Amer. 58, 1308-1310.
- Dooling, R.J., and Searcy, M.H. (1981) Amplitude modulation thresholds for the parakeet (*Melopsittacus undulatus*). J. Comp. Physiol. 143, 383-388.
- Hienz, R.D., Sinnott, J.M., and Sachs, M.B. (1980) Auditory intensity discrimination in blackbirds and pigeons. J. Comp. Physiol. Psychol. 94, 993-1002.
- Okanoya, K., and Dooling, R.J. (1985) Colony differences in auditory thresholds in the canary. J. Acoust. Soc. Amer. 78, 1170-1176.

Table B11-0. Intensity discrimination thresholds as a function of sound intensity in several bird species.

Stimulus Level (dB SPL)	Intensity Discrimination Threshold (dB)					
	1	2	3	4	5	6
20	6.4	5.6	6.1	7.4		
30	5.5	5.3	4.3	5.9		
40	4.1	5.1	3.6	3.5	1.3	
50	3	4.5	2.7	2.9	1.46	
60	2.7				1.34	2.85
70	3				1.24	1.43
80						1.06
85						1.09
90						1.08

Notes:

1- Instrumental shock avoidance conditioning using a modified descending method of limits. Restrained animals trained to avoid shock for a change in intensity by biting a bar. Means: N=3.

Signal was 2.86 kHz tone, 100 msec in duration, 20 msec rise/fall times, spaced 400 msec apart. Conditioned stimulus was an alternation between the standard and a comparison intensity.

2-4- Operant conditioning for a food reward using the method of constant stimuli. Data were averaged over three male redwings, three female redwings, two male brown-headed cowbirds, and two white Carneaux pigeons. Some animals were tested with a go, no-go procedure, and others were tested with a go-left, go-right procedure. There were no consistent differences in intensity discrimination measured across methods, species, or sexes.

The background stimuli were tones, 250 msec in duration with 20 msec rise/fall times, separated by 250 msec of silence. Signals consisted of the pulsed tones alternating in intensity between the standard background intensity and an incremented or decremented intensity. Intensity decrements were difficult for the animals to detect, and failed to maintain conditioned responses in some subjects. The data shown here are for intensity increments.

5- Instrumental shock avoidance using a modified method of limits. Restrained animals trained to bite a bar upon stimulus presentation in order to avoid shock. Means: N=5.

Animals were presented with continuous broad band noise, and the signal consisted of sinusoidal amplitude modulation of the noise carrier (at 40 Hz and below). The intensity discrimination threshold is the difference, in dB, between the sound intensities at the peak and trough of the modulated envelope.

6- Operant conditioning for a food reward using a descending method of limits psychophysical procedure. Means: N=3.

A broad band noise was presented continuously, and the signal consisted of 70 msec increments (20 msec rise/fall times) repeated five times per sec, produced by coherent noise addition. These data show that the Millbrook colony canaries have normal intensity discrimination thresholds, in spite of poor high frequency hearing.

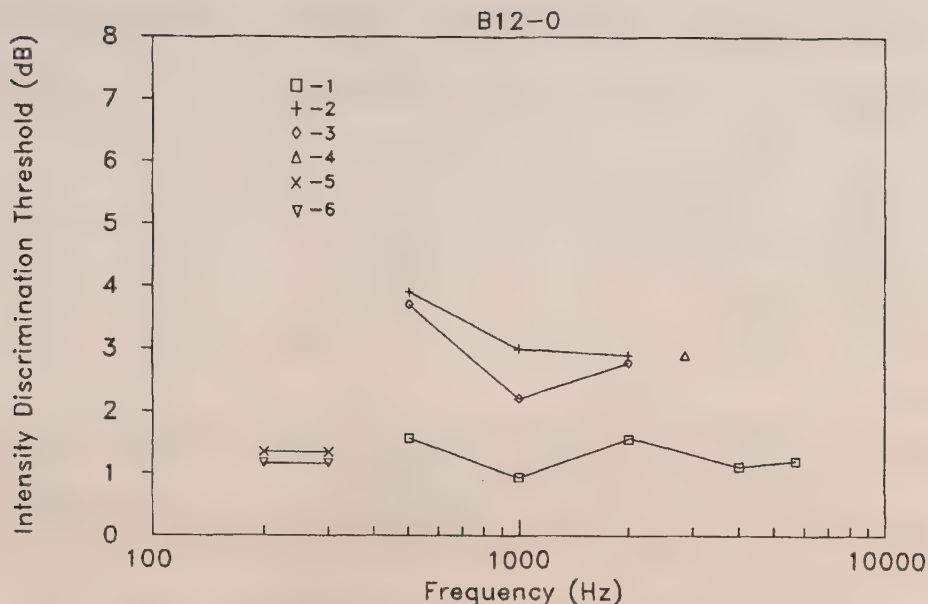


Fig. B12-0. Pure tone intensity discrimination thresholds as a function of frequency in several bird species.

- 1- *Melopsittacus undulatus* - parakeet (Dooling and Searcy, 1979)
- 2- *Agelaius phoeniceus* and *Molothrus ater* - blackbirds (Hienz, Sinnott and Sachs, 1980)
- 3- *Columba livia* - pigeon (Hienz, Sinnott, and Sachs, 1980)
- 4- *Melopsittacus undulatus* - parakeet (Dooling and Saunders, 1975)
- 5- *Melopsittacus undulatus* - parakeet (Dooling and Searcy, 1981)
- 6- *Serinus canarius* - canary, Belgian waterschlager, Millbrook colony (Okanoya and Dooling, 1985)

References:

- Dooling, R.J., and Saunders, J.C. (1975) Auditory intensity discrimination in the parakeet (*Melopsittacus undulatus*). *J. Acoust. Soc. Amer.* 58, 1308-1310.
- Dooling, R.J., and Searcy, M.H. (1979) The relation among critical ratios, critical bands, and intensity difference limens in the parakeet (*Melopsittacus undulatus*). *Bull. Psycho. Soc.* 13, 300-302.
- Dooling, R.J., and Searcy, M.H. (1981) Amplitude modulation thresholds for the parakeet (*Melopsittacus undulatus*). *J. Comp. Physiol.* 143, 383-388.
- Hienz, R.D., Sinnott, J.M., and Sachs, M.B. (1980) Auditory intensity discrimination in blackbirds and pigeons. *J. Comp. Physiol. Psychol.* 94, 993-1002.
- Okanoya, K., and Dooling, R.J. (1985) Colony differences in auditory thresholds in the canary. *J. Acoust. Soc. Amer.* 78, 1170-1176.

Table B12-0. Pure tone intensity discrimination thresholds as a function of frequency in several bird species.

Frequency (Hz)	Intensity Discrimination Threshold (dB)					
	1	2	3	4	5	6
500	1.57	3.9	3.7			
1000	0.93	3	2.2			
2000	1.56	2.9	2.78			
2860				2.9		
4000	1.11					
5700	1.2					
noise					1.35	1.17

Notes:

1- Instrumental shock avoidance using the method of limits. A continuous pure tone was presented at 55 dB SPL, and the signal consisted of a 500 msec increment with 50 msec rise/fall times, repeated once per sec. Means: N=2.

2- Operant conditioning for a food reward using the method of constant stimuli. Average data for three male redwings, three female redwings, and two male brown-headed cowbirds. There were no consistent differences in intensity discrimination measured across species, or sexes.

The background stimuli were tones, 250 msec in duration with 20 msec rise/fall times, separated by 250 msec of silence. Signals consisted of the pulsed tones alternating in intensity between the standard background intensity and an incremented intensity. 40 to 60 dB sensation level.

3- Same as for #2. N=2 white Carneaux pigeons.

4- Instrumental shock avoidance conditioning using a modified descending method of limits. Restrained animals trained to avoid shock during a change in intensity by biting a bar. Means: N=3.

Signal was 2.86 kHz tone, 100 msec in duration, 20 msec rise/fall times, spaced 400 msec apart. Conditioned stimulus was an alternation between the standard and a comparison intensity. 50-70 dB sensation level.

5- Instrumental shock avoidance using a modified method of limits. Restrained animals trained to bite a bar upon stimulus presentation in order to avoid shock. Means: N=5.

Animals were presented with continuous broad band noise, and the signal consisted of sinusoidal amplitude modulation of the noise carrier (at 40 Hz and below). The intensity discrimination threshold is the difference, in dB, between the sound intensities at the peak and trough of the modulated envelope. 40-70 dB sensation level.

6- Operant conditioning for a food reward using a descending method of limits psychophysical procedure. Means: N=3.

A continuous broad band noise was presented, and the signal consisted of 70 msec increments (20 msec rise/fall times) repeated five times per sec, produced by coherent noise addition. 30-50 dB sensation level.

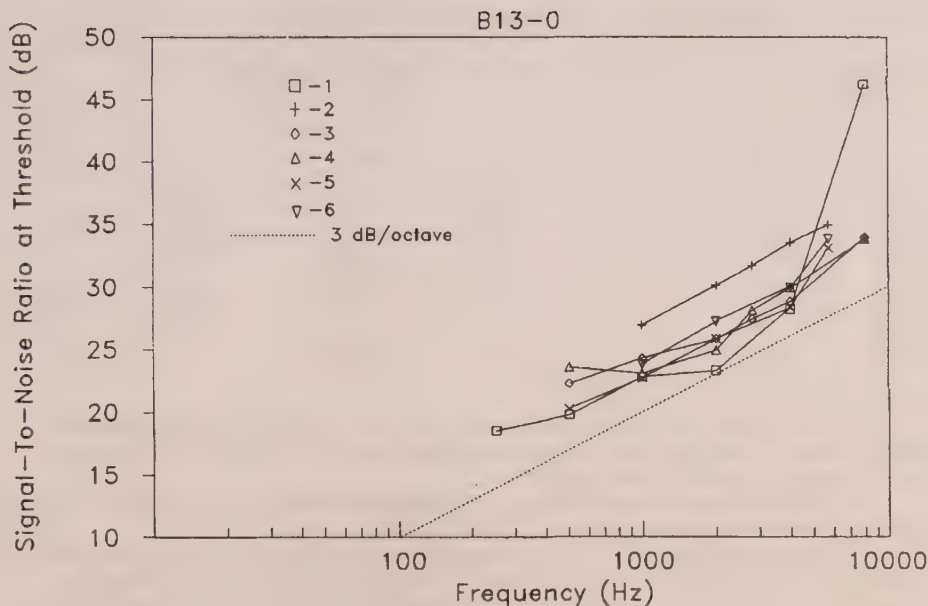


Fig. B13-0. Critical masking ratios for several bird species.

- 1- *Columba livia* - pigeon (Hienz and Sachs, 1987)
- 2- *Serinus canarius* - canary (Okanoya and Dooling, 1987a)
- 3- *Melospiza melodia* - song sparrow (Okanoya and Dooling, 1987a, 1988)
- 4- *Melospiza georgiana* - swamp sparrow (Okanoya and Dooling, 1987a, 1988)
- 5- *Sturnus vulgaris* - starling (Okanoya and Dooling, 1987a, and Dooling, Okanoya, Downing, and Hulse, 1986)
- 6- *Taeniofigia guttata* - zebra finch (Okanoya and Dooling, 1987a)

References:

- Dooling, R.J., Okanoya, K., Downing, J., and Hulse, S. (1986) Hearing in the starling (*Sturnus vulgaris*): Absolute thresholds and critical ratios. *Bull. Psychonom. Soc.* 24, 462-464.
- Hienz, R.D., and Sachs, M.B. (1987) Effects of noise on pure-tone thresholds in blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) and pigeons (*Columba livia*). *J. Comp. Psychol.* 101, 16- 24.
- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Okanoya, K., and Dooling, R.J. (1988) Hearing in the swamp sparrow (*Melospiza Georgiana*) and the song sparrow (*Melospiza Melodia*). *Anim. Behav.* 36, in press.

Table B13-0. Critical masking ratios for several bird species.

Frequency (Hz)	Signal-to-Noise Ratio at Threshold (dB)					
	1	2	3	4	5	6
250	18.5					
500	19.8		22.3	23.6	20.3	
1000	22.8	26.9	24.3	23.1	22.7	23.8
2000	23.3	30.1	25.8	24.9	25.8	27.2
2800		31.7	27.4	28.1		
4000	28.2	33.5	28.8	29.9	28.3	29.9
5700		34.9			33.1	33.8
8000	46.2		33.9	33.8		

Notes:

1- Operant conditioning for food reward (go, no-go) using a modified method of constant stimuli. Masking noise presented continuously at 25 dB SPL per Hz (spectrum level). Means: N=2 white Carneaux pigeons.

2- Operant conditioning for food reward using an adaptive tracking psychophysical procedure. Continuous noise at about 43 dB SPL per Hz. N=1

3- Operant conditioning for food reward using an adaptive tracking psychophysical procedure. Continuous noise ranging between 26 and 43 dB SPL per Hz. Data are an average of the data for one male from Okanoya and Dooling (1987a), and two others from Okanoya and Dooling (1988).

4- Same as #3.

5- Operant conditioning for food reward using an adaptive tracking psychophysical procedure. Continuous noise ranging between 26 and 43 dB SPL per Hz. Data are an average of the data for one male from Okanoya and Dooling (1987a), and one other from Dooling, Okanoya, Downing, and Hulse (1986).

6- Operant conditioning for food reward using an adaptive tracking psychophysical procedure. Continuous noise at about 43 dB SPL per Hz. N=1.

Compare these data with those for other bird species in Fig. B14-0 showing unusual critical masking ratio functions.

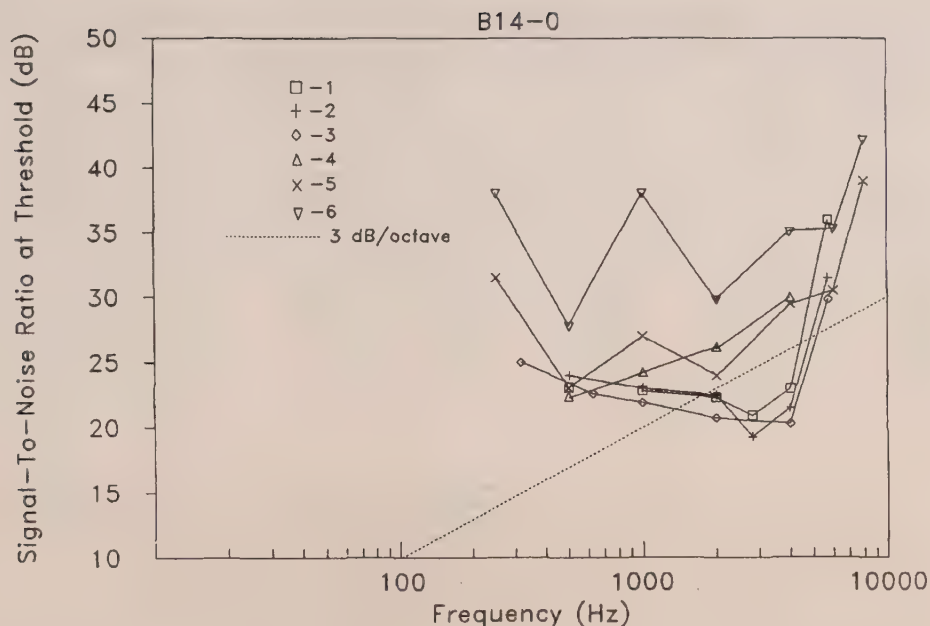


Fig. B14-0. Critical masking ratios for the parakeet and several other bird species.

- 1- *Melopsittacus undulatus* - parakeet (Okanoya and Dooling, 1987a)
- 2- *Melopsittacus undulatus* - parakeet (Dooling and Saunders, 1975)
- 3- *Melopsittacus undulatus* - parakeet (Saunders, Rintelmann, and Bock, 1979)
- 4- *Nymphicus hollandicus* - cockatiel (Okanoya and Dooling, 1987a)
- 5- *Agelaius phoeniceus* - red-winged blackbirds and *Molothrus ater* - brown-headed cowbird (Hienz and Sachs, 1987), continuous noise.
- 6- Same as #4, pulsed noise

References:

- Dooling, R.J., and Saunders, J.C. (1975) Hearing in the parakeet (*Melopsittacus undulatus*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations. *J. Comp. Physiol. Psychol.* 88, 1-20.
- Hienz, R.D., and Sachs, M.B. (1987) Effects of noise on pure-tone thresholds in blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) and pigeons (*Columba livia*). *J. Comp. Psychol.* 101 16-24.
- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Saunders, J.C., Rintelmann, W.F., and Bock, G.R. (1979) Frequency selectivity in bird and man: A comparison among critical ratios, critical bands and psychophysical tuning curves. *Hear. Res.* 1, 303-323.

Table B14-0. Critical masking ratios for the parakeet and several other bird species.

Frequency (Hz)	Signal-to-Noise Ratio at Threshold (dB)					
	1	2	3	4	5	6
250					31.5	38
315			25			
500	23.1	24		22.4	23	27.8
630			22.6			
1000	22.8	23	21.9	24.2	27	38
2000	22.3	22.5	20.7	26.2	24	29.8
2800	20.9	19.3				
4000	23	21.5	20.3	30	29.5	35
5700	36	31.5	29.8			
6000					30.5	35.3
8000					39	42.2

Notes:

1- Operant conditioning for food reward using an adaptive tracking psychophysical procedure. Continuous noise at about 43 dB SPL per Hz. Means: N=2, each not tested at all frequencies.

2- Instrumental shock avoidance conditioning using the method of limits psychophysical procedure. A restrained bird was trained to bite a rod upon the presentation of a tone in order to avoid shock. Continuous noise at 27.4 dB SPL per Hz. Means: N=4 6-16 weeks old birds.

3- Same methods as #2. Continuous noise at 30 dB SPL per Hz (at 630, 1000, 2000, and 4000 Hz), and 50 dB per Hz (at 315 and 5700 Hz). Means: N=6.

4- Operant conditioning for food reward using an adaptive tracking psychophysical procedure. Continuous noise at about 43 dB SPL per Hz. N=1.

5- Operant conditioning for food reward (go-left, go-right) using a modified method of constant stimuli. Masking noise presented continuously at 24 dB SPL per Hz (spectrum level). Means: N=8 redwings and N=3 cowbirds.

6- Operant conditioning for food reward (go left, go-right) using a modified method of constant stimuli. Masking noise pulsed "on" with the tone signal for 1 sec at 24 dB SPL per Hz (spectrum level). Means: N=8 redwings and N=3 cowbirds. Note that critical ratios are larger for the pulsed noise condition.

Compare these rather unusual critical masking ratio functions with those for other species in Fig. B13-0.

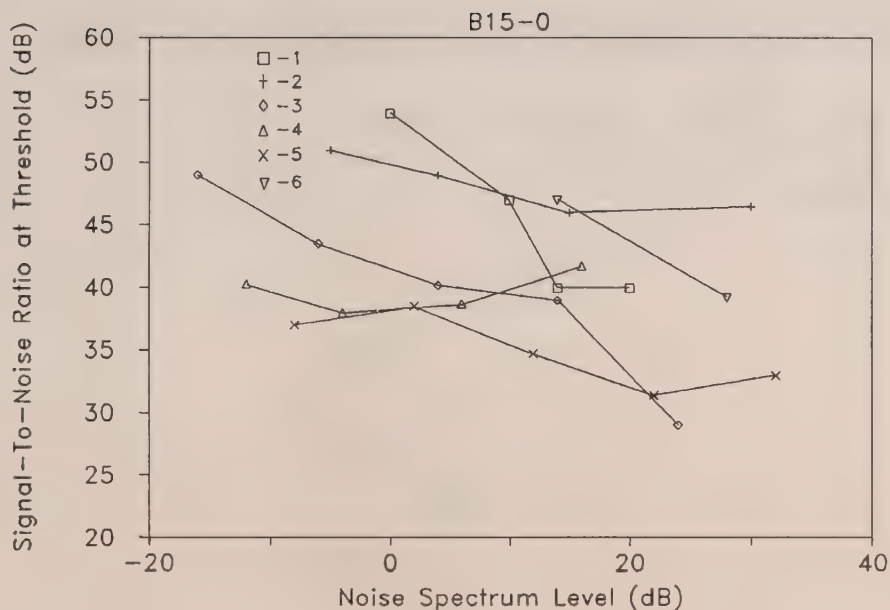


Fig. B15-0. Critical masking ratios as functions of noise spectrum level for blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) (Hienz and Sachs, 1987).

- 1- 500 Hz signal frequency
- 2- 1000 Hz
- 3- 2000 Hz
- 4- 4000 Hz
- 5- 6000 Hz
- 6- 8000 Hz

Reference:

Hienz, R.D., and Sachs, M.B. (1987) Effects of noise on pure-tone thresholds in blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) and pigeons (*Columba livia*). J. Comp. Psychol. 101, 16-24.

Table B15-0. Critical masking ratios as functions of noise spectrum level for blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) (Hienz and Sachs, 1987).

Noise Spectrum Level (dB SPL/Hz)	Signal-to-Noise Ratio at Threshold (dB)					
	1	2	3	4	5	6
-16			49			
-12				40.3		
-8					37	
-6			43.5			
-5		51				
-4				38		
0	54					
2					38.5	
4		49	40.2			
6				38.7		
10	47					
12					34.7	
14	40		39			47
15		46				
16				41.8		
20	40					
22					31.4	
24			29			
28						39.2
30		46.5				
32					33	

Notes:

Operant conditioning for food reward (go, no-go) using a modified method of constant stimuli. Masking noise pulsed on with the signal at 25 dB SPL per Hz (spectrum level). Data are averages over all redwings and cowbirds in the study (N=11).

Slopes are significantly different from zero at 500 Hz and 2000 Hz where increasing noise level leads to smaller critical ratios. Note the "jagged" nature of the critical ratio function for pulsed noise conditions in blackbirds (shown in Fig. B14-0, #5 and #6). The dips at 500 Hz and 2000 Hz would tend to disappear if the function were plotted for noise spectrum levels below 20 dB SPL. The origin of these nonlinear effects are not known. They could possibly be explained as a narrowing of the auditory filter at these two frequencies, at high intensities. Another possible explanation is that the just-discriminable change in intensity declines with intensity (misses Weber's Law) specifically at 500 and 2000 Hz. Neither possibility seems very likely.

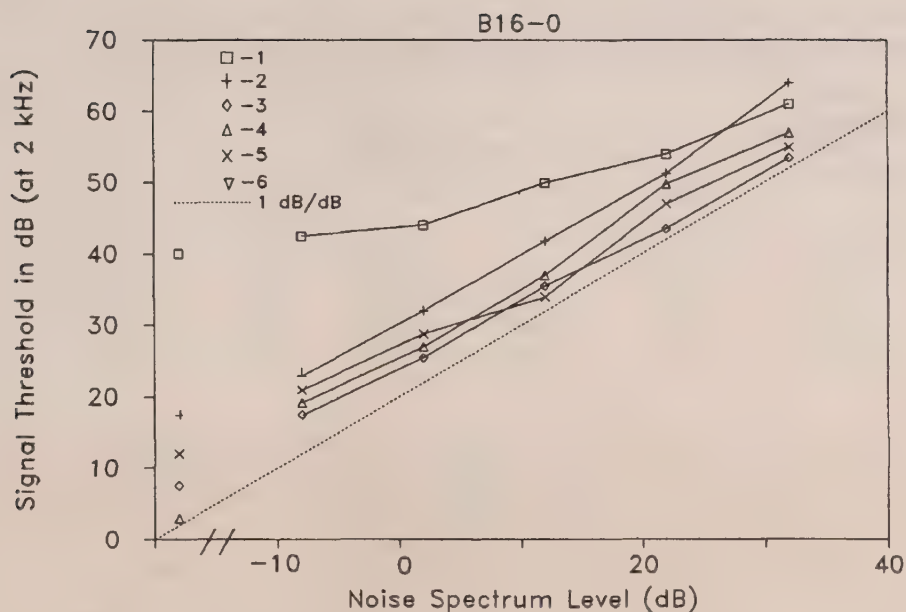


Fig. B16-0. The effect of masking noise level on tone detection threshold in the parakeet, song sparrow, swamp sparrow, and two canary strains (Okanoya and Dooling, 1985).

- 1- *Serinus canarius* - canary, Belgian waterschlager strain, Millbrook colony
- 2- *Serinus canarius* - canary, German roller strain
- 3- *Melopsittacus undulatus* - parakeet or budgerigar
- 4- *Zonotrichia melodia* - song sparrow
- 5- *Zonotrichia georgiana* - swamp sparrow

Dashed line indicates unity slope.

Reference:

Okanoya, K., and Dooling, R.J. (1985) Colony differences in auditory thresholds in the canary. *J. Acoust. Soc. Amer.* 78, 1170-1176.

Table B16-0. The effect of masking noise level on tone detection threshold in the parakeet, song sparrow, swamp sparrow, and two canary strains.

Noise Spectrum Level (dB SPL)	Signal Threshold (dB SPL)				
	1	2	3	4	5
Quiet	40	17.5	7.5	3	12
-8	42.5	23	17.5	19.2	21
2	44	32	25.5	27	28.8
12	50	41.8	35.5	37	34
22	54	51.3	43.5	49.8	47
32	61	64	53.5	57	55

Notes:

Operant conditioning for food reward using the staircase psychophysical procedure. Animals were trained to peck one key (observation key) repeatedly when a 2 kHz tone was absent, and to switch responses to another key when the tone was present. Noise was wide band and continuous at the indicated spectrum levels (dB SPL/Hz). See additional data for some of the same species in Figs. B17-0 and B18-0.

1- Four adult Belgian waterschlager canaries from the colony maintained at Millbrook, NY (Rockefeller University field research station). Canaries from this colony have been used extensively in studies of vocal learning (e.g. Nottebohm, 1980). They have been shown to have poor high frequency hearing compared with other strains. The present data suggest a rather shallow growth-of-masking function.

2- Means: N=3.

3- N=1.

4- N=1.

5- N=1.

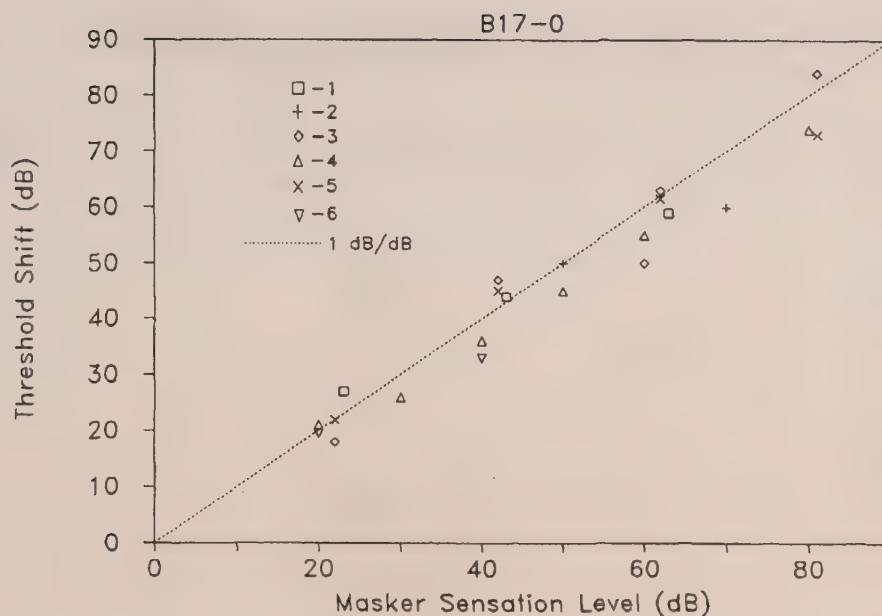


Fig. B17-0. The relation between masker sensation level and the amount of masking for tones masked by noise in *Melopsittacus undulatus* (parakeet) (Saunders and Pallone, 1980).

- 1- 630 Hz tone signal
- 2- 1000 Hz
- 3- 1600 Hz
- 4- 2500 Hz
- 5- 3500 Hz
- 6- 5000 Hz

The dashed line indicates unity slope.

Reference:

Saunders, J.C., and Pallone, R.L. (1980) Frequency selectivity in the parakeet studied by isointensity masking contours. *J. Exp. Biol.* 87, 331-342.

Table B17-0. The relation between masker sensation level and the amount of masking for tones masked by noise in *Melopsittacus undulatus* (parakeet) (Saunders and Pallone, 1980).

Masker Sensation Level (dB)	Amount of Masking (or Threshold Shift) (dB)					
	1	2	3	4	5	6
20				21		19.5
22			18		22	
23	27					
30				26		
40				36		33
42			47		45	
43	44					
50		50		45		
60			50	55		
62			63		61.5	
63	59					
70		60				
80				74		
81			84		73	

Notes:

Instrumental shock avoidance using a modified method of limits. Restrained birds were trained to bite a bar to avoid shock in the presence of the signal tone. Means: N=4.

These data are from a study of tone-on-tone masking in which the tone masker was presented continuously, and the signal tone was presented briefly with 50 msec rise/fall times. Masker frequency and level were fixed, and the masked threshold for a signal tone determined as a function of signal frequency. The data shown here are the masked thresholds for the case in which signal frequency equals masker frequency (maximum masking).

In these coordinates, the slope of the best-fitting linear function is 0.92. (The function drawn in the figure is not a best fit; it simply demonstrates a unity slope.) This means that threshold shifts are slightly smaller at the higher intensities. This could be caused by a reduction in the intensity discrimination threshold at high intensities (see Fig. B11-0). This represents a very "near miss" to Weber's Law, as has been observed in humans and other vertebrates.

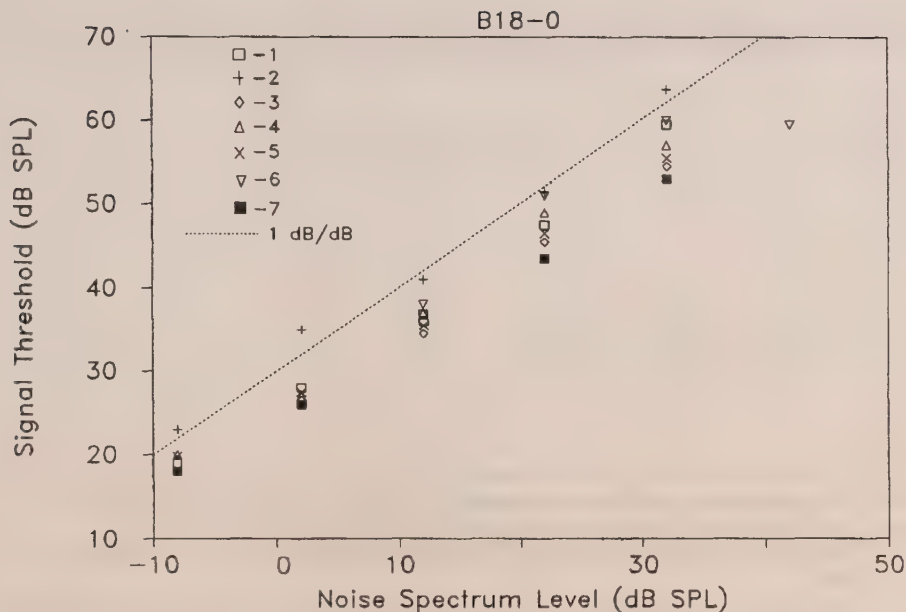


Fig. B18-0. Masked threshold for tone detection as a function of masking noise level in seven bird species (Okanoya and Dooling, 1987a and 1988*).

- 1- *Nymphicus hollandicus* - cockatiel
- 2- *Serinus canarius* - canary
- 3- *Sturnus vulgaris* - European starling
- 4- **Melospiza melodia* - song sparrow
- 5- **Melospiza georgiana* - swamp sparrow
- 6- *Taeniofigia guttata* - zebra finch
- 7- *Melopsittacus undulatus* - parakeet

References:

- Okanoya, K., and Dooling, R.J. (1987a) Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.* 101, 7-15.
- Okanoya, K., and Dooling, R.J. (1988) Hearing in the swamp sparrow (*Melospiza Georgiana*) and the song sparrow (*Melospiza Melodia*). *Anim. Behav.* 36, in press.

Table B18-0. Masked threshold for tone detection as a function of masking noise level in seven bird species (Okanoya and Dooling, 1987a, 1988).

Mask Noise Spectrum Level- dB SPL	Masked Signal Threshold (dB SPL)						
	1	2	3	4	5	6	7
-8	19	23	18	20	21		18
2	28	35	26.5	27	28.5		26
12	36.8	41	34.5	37.5	36	38	36
22	47.5	51.5	45.5	49.5	47	51	43.5
32	59.5	63.7	54.5	57.5	55.5	60	53
42						69.5	

Notes:

Operant conditioning for food reward using the staircase psychophysical procedure. Animals were trained to peck one key (observation key) repeatedly when a tone was absent, and to switch responses to another key when a tone was present.

Broad band, continuous masking noise. Signal frequency at 2 kHz. One male of each species.

4-5- Data for song sparrow and swamp sparrow averaged over the two studies cited.

Slopes of best-fitting linear functions for each species range between 0.881 and 1.048. The average slope is less than unity, indicating slightly reduced critical masking ratios toward the higher intensities. (See Notes for Fig. 17-0.)

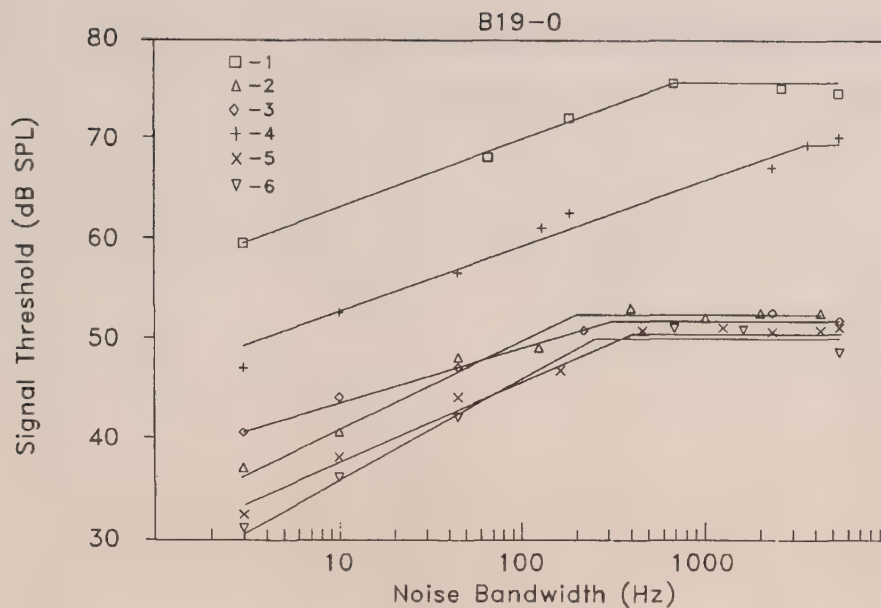


Fig. B19-0 Masked tone threshold as a function of masker bandwidth in *Melopsittacus undulatus* (parakeet) (Saunders, Denny, and Bock, 1978).

- 1- 315 Hz signal frequency
- 2- 630 Hz
- 3- 1000 Hz
- 4- 2000 Hz
- 5- 4000 Hz
- 6- 5700 Hz

Reference:

Saunders, J.C., Denny, R.M., and Bock, G.R. (1978) Critical bands in the parakeet (*Melopsittacus undulatus*). J. Comp. Physiol. 125, 359-365.

Table B19-0. Masked tone threshold as a function of masker bandwidth in *Melopsittacus undulatus* (parakeet) (Saunders, Denny, and Bock, 1978).

Noise Bandwidth (Hz)	Masked Threshold (dB SPL)					
	1	2	3	4	5	6
3	59.5	47	40.5	37	32.4	31
10		52.5	44	40.5	38	36
45		56.5	47	48	44	42
66	68					
125				49		
130		61				
164					46.7	
185	72	62.5				
220			50.7			
400				53		
460					50.7	
690	75.5					51
1020				52		
1260					51	
1630						50.8
2020				52.5		
2340		67	52.5		50.6	
2650	75					
3650		69.3				
4270				52.5	50.7	
5420	74.5	70	51.7		51	48.5

Notes:

Instrumental shock avoidance using a modified method of limits. Restrained animals were trained to bite a bar in order to avoid shock in the presence of the signal tone. Means: N=6.

Continuous noise masker, 4 sec pure tone signal, 50 msec rise/fall times. Noise levels about 30 dB SPL/Hz.

Critical bandwidths determined directly using noise bands of different bandwidth centered on the signal frequency as maskers. The critical bandwidth was defined as the bandwidth above which the masked tone threshold became independent of bandwidth. The lines drawn are the authors' "best fit" functions. The critical bandwidth values of Fig. B20-0 were derived from these data.

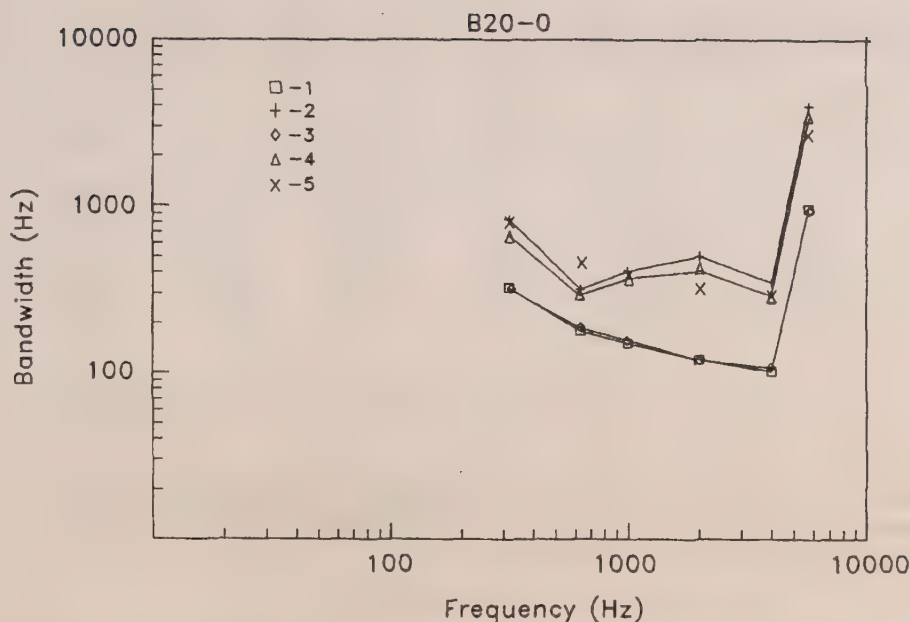


Fig. B20-0. Critical masking bands and critical masking ratios (expressed in Hz) in *Melopsittacus undulatus* (parakeet),

- 1- Critical ratios converted to bandwidths (Hz) (Saunders, Denny, and Bock, 1978)
- 2- Critical bandwidths (Hz) (Saunders, Denny, and Bock, 1978)
- 3- Critical ratios converted to bandwidths (Hz) (Saunders, Rintelmann, and Bock, 1979)
- 4- Critical bandwidths (Hz) (Saunders, Rintelmann, and Bock, 1979)
- 5- Average of #1 and #3 multiplied by 2.5

References:

- Saunders, J.C., Denny, R.M., and Bock, G.R. (1978) Critical bands in the parakeet (*Melopsittacus undulatus*). J. Comp. Physiol. 125, 359-365.
- Saunders, J., Rintelmann, W., and Bock, G. (1979) Frequency selectivity in bird and man: A comparison among critical ratios, critical bands and psychophysical tuning curves. Hear. Res. 1, 303-323.

Table B20-0. Critical masking bands and critical masking ratios (expressed in Hz) in *Melopsittacus undulatus* (parakeet).

Frequency (Hz)	Bandwidth (Hz)				
	1	2	3	4	5
315	323	832	316	646	799
630	178	316	182	302	450
1000	151	407	155	372	383
2000	120	501	117	407	296
4000	102	347	107	269	261
5700	955	3981	950	3090	2381

Notes:

Instrumental shock avoidance using a modified method of limits. Restrained animals were trained to bite a bar in order to avoid shock in the presence of the signal tone.

1- Continuous, broad band noise masker, 4 sec pure tone signal, 50 msec rise/fall times. Noise levels about 30 dB SPL/Hz. Critical ratio bandwidths are the critical masking ratio values in dB (signal-to-noise ratio at masked threshold) converted into an equivalent bandwidth in Hz. Means: N=6.

$$CR_{(dB)} = 10 \log(BW_{(Hz)}), \text{ or } BW_{(Hz)} = 10^{(CR/10)}$$

2- Critical bandwidths determined directly using noise bands of different bandwidth centered on the signal frequency as maskers (See Fig. B19-0). The critical bandwidth was defined as the bandwidth above which the masked tone threshold became independent of bandwidth. Same subjects as in #1.

3- Same methods as #1. N=6. These data also presented as critical ratios (in dB) in Fig. B14-0.

4- Same methods as #2. Same subjects as in #3.

5- For comparison with the critical bandwidths, the average critical masking ratio bandwidths (from #1 and #3) were multiplied by 2.5. This factor difference between the two measures of frequency selectivity is due in large part to the size of the intensity discrimination threshold for the parakeet (Dooling and Searcy, 1979). This same factor separates critical band and critical ratio bandwidth estimates in humans.

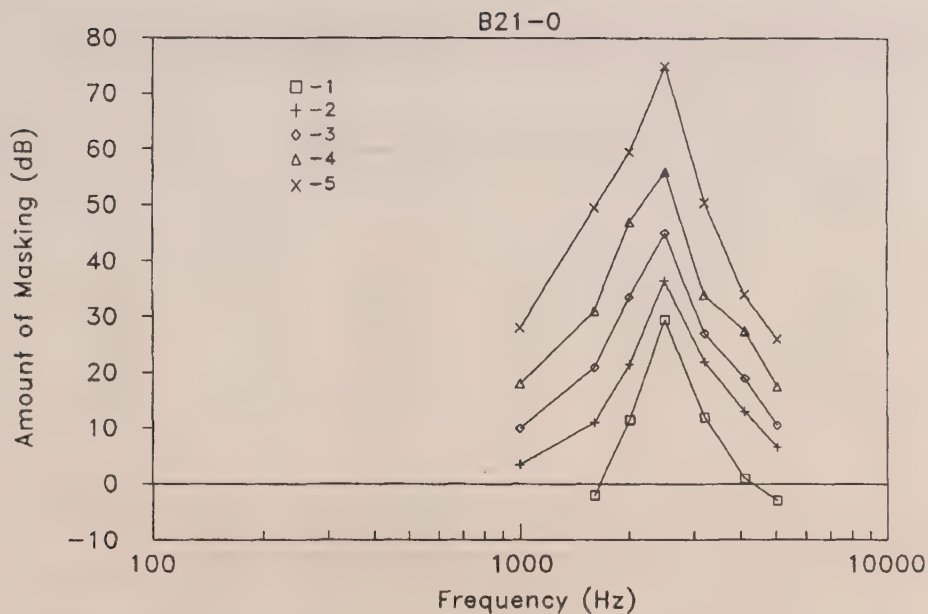


Fig. B21-0. Masked thresholds for tones in the presence of a 2500 Hz tonal masker at different levels, in *Melopsittacus undulatus* (parakeet) (Saunders and Pallone, 1980).

- 1- 36 dB SPL masker level
- 2- 46 dB
- 3- 56 dB
- 4- 66 dB
- 5- 86 dB

Reference:

Saunders, J. and Pallone, R. (1980) Frequency selectivity in the parakeet studied by isointensity masking contours. *J. Exp. Biol.* 87, 331-342.

Table B21-0. Masked thresholds for tones in the presence of a 2500 Hz tonal masker at different levels, in *Melopsittacus undulatus* (parakeet) (Saunders and Pallone, 1980).

Signal Frequency (Hz)	Threshold Shift (Masking Effect) (dB)				
	1	2	3	4	5
1000	3.5	10	18	28	
1600	-2	11	21	31	49.5
2000	11.5	21.5	33.5	47	59.5
2500	29.5	36.5	45	56	75
3200	12	22	27	34	50.5
4100	1	13	19	27.5	34
5000	-3	6.5	10.5	17.5	26

Notes:

Instrumental shock avoidance using a method of limits. Restrained birds were trained to bite a bar in the presence of the signal in order to avoid shock. Masker tone on continuously. Tone signal had 50 msec rise/fall times. Means: N=4.

The authors point out that these functions are relatively symmetrical and do not change shape significantly at different masker levels. Similar data on masker intensity were obtained for maskers at 630, 1000, 1600, 3500, and 5000 Hz (not plotted here). The general conclusions are the same as for the data plotted here. These masking curves, collapsed across masker levels, are given in Fig. B22-0. The nearly linear effect of masker level on masked threshold at the frequency of the masker is shown in Fig. B17-0.

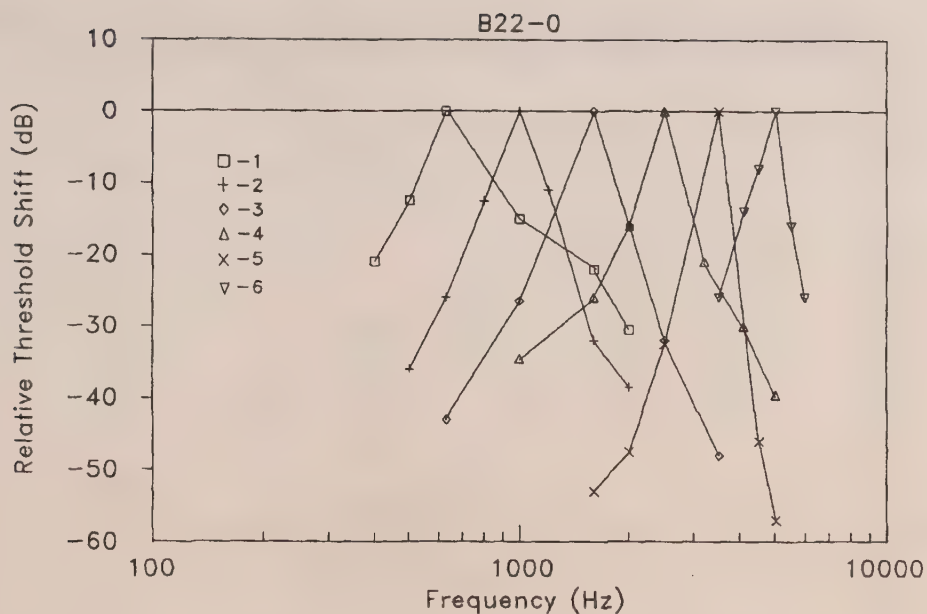


Fig. B22-0. Masked thresholds for tones in the presence of tonal maskers at different frequencies, in *Melopsittacus undulatus* (parakeet) (Saunders and Pallone, 1980).

- 1- 630 Hz masker frequency
- 2- 1000 Hz
- 3- 1600 Hz
- 4- 2500 Hz
- 5- 3500 Hz
- 6- 5000 Hz

Reference:

Saunders, J. and Pallone, R. (1980) Frequency selectivity in the parakeet studied by isointensity masking contours. *J. Exp. Biol.* 87, 331-342.

Table B22-0. Masked thresholds for tones in the presence of tonal maskers at different frequencies, in *Melopsittacus undulatus* (parakeet) (Saunders and Pallone, 1980).

Signal Frequency (Hz)	Relative Threshold Shift (dB)					
	1	2	3	4	5	6
400	-21					
500	-12.5	-36				
630	0	-26	-43			
800		-12.5				
1000	-15	0	-26.5	-34.5		
1200		-11				
1600	-22	-32	0	-26	-53	
2000	-30.5	-38.5	-16	-16	-47.5	
2500			-32	0	-32.5	
3200				-21		
3500			-48		0	-26
4100				-30		-14
4500					-46	-8
5000				-39.5	-57	0
5500						-16
6000						-26

Notes:

Instrumental shock avoidance using a method of limits. Restrained birds were trained to bite a bar in the presence of the signal in order to avoid shock. Masker tone presented continuously. Tone signal had 50 msec rise/fall times. Means: N=4.

These data are averaged over several different masker levels (See Fig. B21-0), and are shown relative to the greatest amount of masking (set here to 0 dB). The negative values indicate the decline of the masking effect as the signal frequency is moved away from the masker frequency. See Fig. B17-0 for the effect of masker level on signal threshold at the masker frequency.

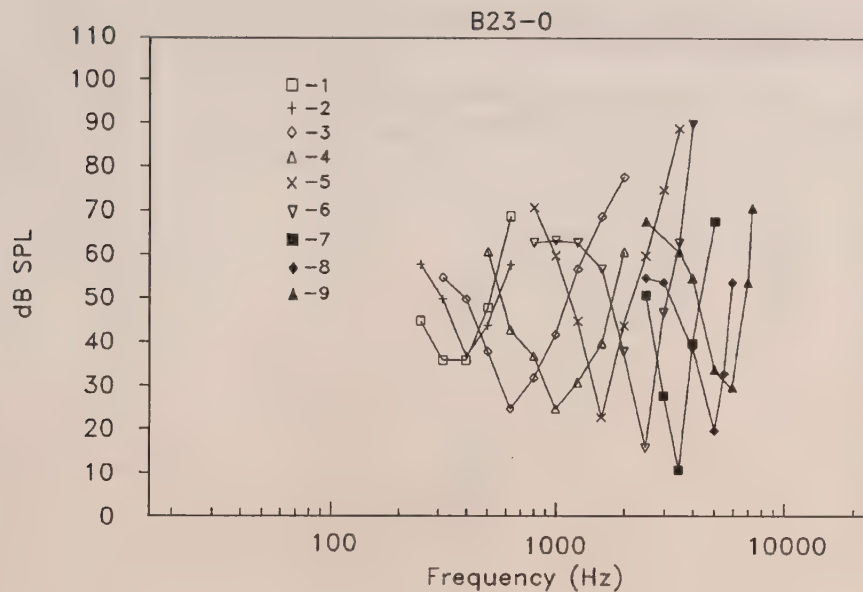


Fig. B23-0. Psychophysical tuning curves for *Melopsittacus undulatus* (parakeet) (Saunders, Rintelmann, and Bock, 1979).

- 1- 315 Hz signal frequency
- 2- 400 Hz
- 3- 630 Hz
- 4- 1000 Hz
- 5- 1600 Hz
- 6- 2500 Hz
- 7- 3500 Hz
- 8- 5000 Hz
- 9- 6000 Hz

Reference:

Saunders, J.C., Rintelmann, W.F., and Bock, G.R. (1979) Frequency selectivity in bird and man: A comparison among critical ratios, critical bands and psychophysical tuning curves. *Hear. Res.* 1, 303-323.

Table B23-0. Psychophysical tuning curves for *Melopsittacus undulatus* (parakeet) (Saunders, Rintelmann, and Bock, 1979).

Signal Frequency (Hz)	Masker Level at Signal Threshold (dB SPL)								
	1	2	3	4	5	6	7	8	9
250	45	58							
315	36	50	55						
400	36	37	50						
500	48	44	38	61					
630	69	58	25	43					
800			32	37	71	63			
1000			42	25	60	63.5			
1250			57	31	45	63			
1600			69	40	23	57			
2000			78	61	44	38			
2500					60	16	51	55	68
3000					75	47	28	54	
3500					89	63	11		61
4000						90	40	39	55
5000							68	20	34
5500								33	
6000								54	30
7000									54
7300									71

Notes:

Instrumental shock avoidance conditioning using the method of limits psychophysical procedure. A restrained bird was trained to bite a rod upon the presentation of a tone in order to avoid shock. Continuous masker tone. Signal level fixed at 10 dB sensation level. Means: N=6.

These functions show the following Q_{10dB} values (where Q_{10dB} is defined as the center frequency of the filter function divided by the bandwidth 10 dB above best threshold):

Center Frequency (Hz)	Q_{10dB}
315	1.4
400	2.1
630	2.0
1000	2.4
1600	4.7
2500	5.6
3500	9.5
5000	5.3
6000	3.3

Note that these show a tuning maximum at 3500 Hz, the same frequency region showing the smallest critical bandwidths (Fig. B20-0) and the smallest critical masking ratios (Fig. B14-0).

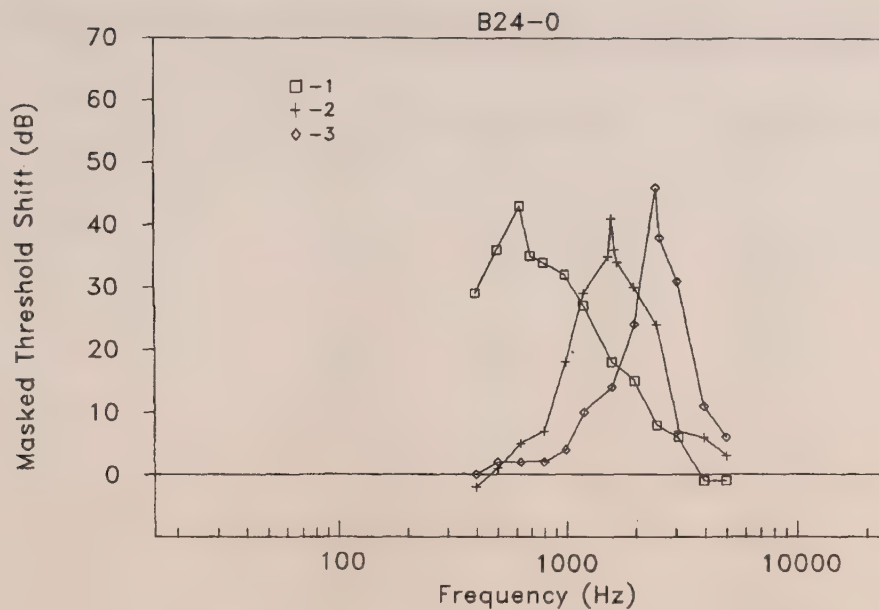


Fig. B24-0. Tone-on-tone masking in *Melopsittacus undulatus* (parakeet) at three masker frequencies (Saunders and Else, 1976).

- 1- 630 Hz masker frequency
- 2- 1600 Hz masker frequency
- 3- 2500 Hz masker frequency

Reference:

Saunders, J.C., and Else, P.V. (1976) Pure tone masking in the parakeet: A preliminary report. Trans. Amer. Acad. Opthal. Oto. 82, 356-362.

Table B24-0. Tone-on-tone masking in *Melopsittacus undulatus* (parakeet) at three masker frequencies (Saunders and Else, 1976).

Signal Frequency (Hz)	Threshold Shift (dB)		
	1	2	3
400	29	-2	0
500	36	1	2
630	43	5	2
700	35		
800	34	7	2
1000	32	18	4
1200	27	29	10
1550		35	
1600	18	41	14
1650		36	
1700		34	
2000	15	30	24
2500	8	24	46
2600			38
3100	6	7	31
4000	-1	6	11
5000	-1	3	6

Notes:

Instrumental shock avoidance conditioning using the method of limits psychophysical procedure. Maskers were continuous pure tones presented at 60 dB SL. Signals were pure tones with 50 msec rise/fall times. Q_{10dB} values are 1.6, 2.8, and 4.3 for the 630, 1600, and 2500 Hz masking curves, respectively.

Similar data are also presented in Saunders (1976).

N=4 for #1 and #3. N=2 for #2.

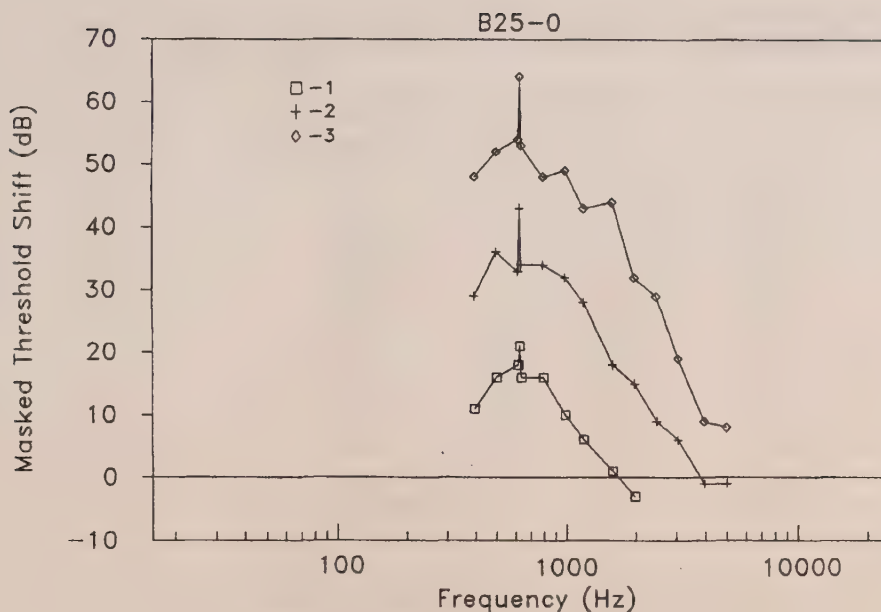


Fig. B25-0. The effects of masker level on tone-on-tone masking in *Melopsittacus undulatus* (parakeet).

- 1- 40 dB SL masker level
- 2- 60 dB SL
- 3- 80 dB SL

Reference:

Saunders, J.C. (1976) The psychophysical analysis of pure-tone masking in the parakeet. In S.K. Hirsh, D.H. Eldridge, I.J. Hirsh, and S.R. Silverman (eds), *Hearing and Davis: Essays Honoring Hallowell Davis*. Washington University Press: Saint Louis, pp. 199-212.

Table B25-0. The effects of masker level on tone-on-tone masking in *Melopsittacus undulatus* (parakeet).

Signal Frequency (Hz)	Masking Effect (dB)		
	1	2	3
400	11	29	48
500	16	36	52
620	18	33	54
630	21	43	64
640	16	34	53
800	16	34	48
1000	10	32	49
1200	6	28	43
1600	1	18	44
2000	-3	15	32
2500		9	29
3100		6	19
4000		-1	9
5000		-1	8

Notes:

Instrumental shock avoidance conditioning using the method of limits psychophysical procedure. Maskers were continuous pure tones presented at 60 dB SL. Signals were pure tones with 50 msec rise/fall times. N=3 for #1. N=4 for #2 and #3.

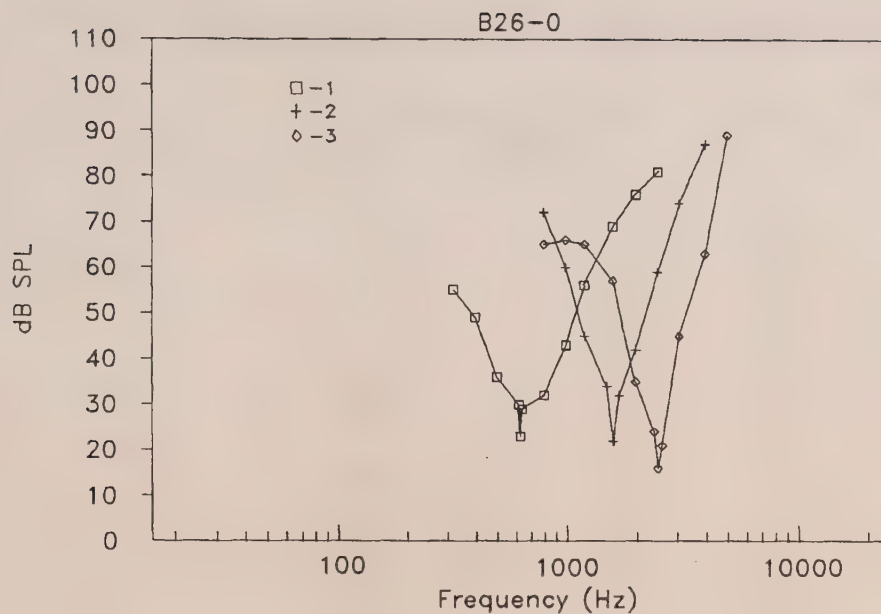


Fig. B26-0. Psychophysical tuning curves for *Melopsittacus undulatus* (parakeet) (Saunders, Else, and Bock, 1978).

- 1- 630 Hz signal frequency
- 2- 1600 Hz
- 3- 2500 Hz

Reference:

Saunders, J.C., Else, P.V., and Bock, G.R. (1978) Frequency selectivity in the parakeet (*Melopsittacus undulatus*) studied with psychophysical tuning curves. *J. Comp. Physiol. Psychol.* 92, 406-415.

Table B26-0. Psychophysical tuning curves for *Melopsittacus undulatus* (parakeet) (Saunders, Else, and Bock, 1978).

Masker Frequency (Hz)	Masker Level at Threshold (dB SPL)		
	1	2	3
320	55		
400	49		
500	36		
620	30		
630	23		
640	29		
800	32	72	65
1000	43	60	66
1200	56	45	65
1500		34	
1600	69	22	57
1700		32	
2000	76	42	35
2400			24
2500	81	59	16
2600			21
3100		74	45
4000		87	63
5000			89

Notes:

Instrumental shock avoidance conditioning using the descending method of limits psychophysical procedure. Maskers were continuous pure tones. Signals were 10 dB SL pure tones with 50 msec rise/fall times. In this paradigm, the signal is fixed in frequency and level, and the masker level required to bring the signal to threshold is measured as a function of masker frequency.

Standard deviations about the mean thresholds ranged between 2.5 and 6.1 dB.

Similar psychophysical tuning curve data (not shown here) were presented in Saunders (1976).

Unmasked thresholds for the parakeet were also given in this study but not plotted in Fig. B3-0.

Means: N=4 for #1, N=5 for #2, N=7 for #3.

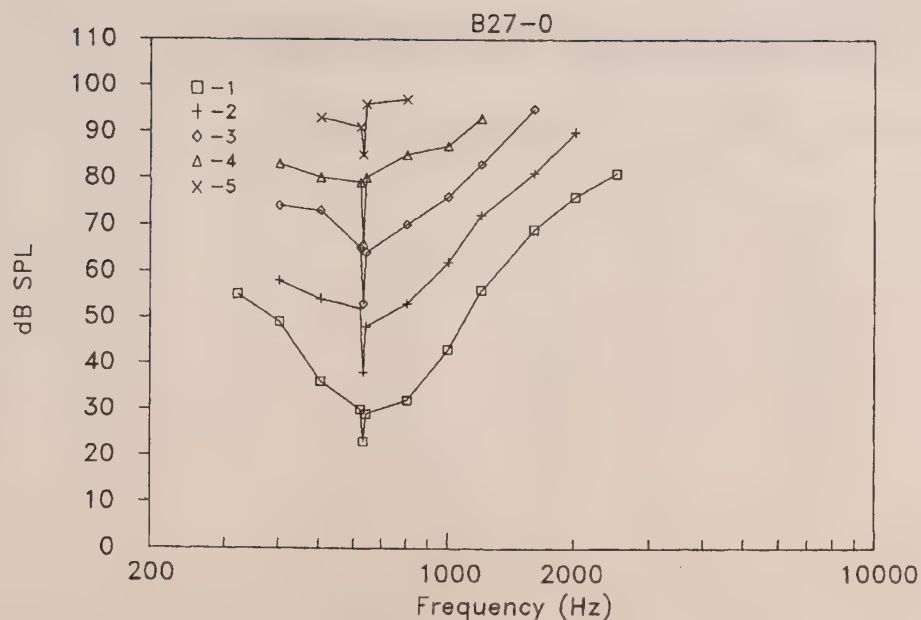


Fig. B27-0. The effect of signal level on psychophysical tuning curves at 630 Hz for *Melopsittacus undulatus* (parakeet) (Saunders, Else, and Bock, 1978).

- 1- 10 dB SL signal level
- 2- 20 dB SL
- 3- 30 dB SL
- 4- 40 dB SL
- 5- 50 dB SL

Reference:

Saunders, J.C., Else, P.V., and Bock, G.R. (1978) Frequency selectivity in the parakeet (*Melopsittacus undulatus*) studied with psychophysical tuning curves. *J. Comp. Physiol. Psychol.* 92, 406-415.

Table B27-0. The effect of signal level on psychophysical tuning curves at 630 Hz for *Melopsittacus undulatus* (parakeet) (Saunders, Else, and Bock, 1978).

Masker Frequency (Hz)	Masker Level at Threshold (dB SPL)				
	1	2	3	4	5
320	55				
400	49	58	74	83	
500	36	54	73	80	93
620	30	52	65	79	91
630	23	38	53	66	85
640	29	48	64	80	96
800	32	53	70	85	97
1000	43	62	76	87	
1200	56	72	83	93	
1600	69	81	95		
2000	76	90			
2500	81				

Notes:

Instrumental shock avoidance conditioning using the descending method of limits psychophysical procedure. Maskers were continuous pure tones. Signals were pure tones with 50 msec rise/fall times. In this paradigm, the signal is fixed in frequency and level, and the masker level required to bring the signal to threshold is measured as a function of masker frequency.

The authors note that these data and those of Figs. B28-0 and B29-0, show that the basic form of the psychophysical tuning curves remain rather constant at different signal levels. In general, the curves are narrowest at low sensation levels and at high signal frequencies. The frequency at which masking is most effective does not shift with changes in signal level, as demonstrated by a detailed analysis of the tuning curve shape at 1600 Hz (not shown here).

Masker level at threshold plotted as a function of signal level is a linear function with a slope of 1.4.

Means: N=4.

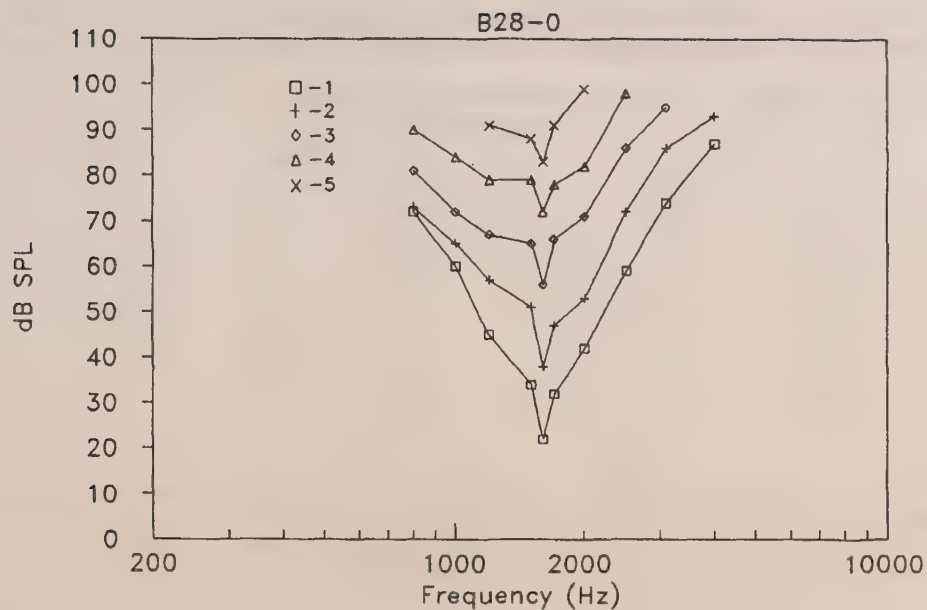


Fig. B28-0. The effect of signal level on psychophysical tuning curves at 1600 Hz for *Melopsittacus undulatus* (parakeet) (Saunders, Else, and Bock, 1978).

- 1- 10 dB SL signal level
- 2- 20 dB SL
- 3- 30 dB SL
- 4- 40 dB SL
- 5- 50 dB SL

Reference:

Saunders, J.C., Else, P.V., and Bock, G.R. (1978) Frequency selectivity in the parakeet (*Melopsittacus undulatus*) studied with psychophysical tuning curves. *J. Comp. Physiol. Psychol.* 92, 406-415.

Table B28-0. The effect of signal level on psychophysical tuning curves at 1600 Hz for *Melospittacus undulatus* (parakeet) (Saunders, Else, and Bock, 1978).

Masker Frequency (Hz)	Masker Level at Threshold (dB SPL)				
	1	2	3	4	5
800	72	73	81	90	
1000	60	65	72	84	
1200	45	57	67	79	91
1500	34	51	65	79	88
1600	22	38	56	72	83
1700	32	47	66	78	91
2000	42	53	71	82	99
2500	59	72	86	98	
3100	74	86	95		
4000	87	93			

Notes:

Instrumental shock avoidance conditioning using the descending method of limits psychophysical procedure. Maskers were continuous pure tones. Signals were pure tones with 50 msec rise/fall times. In this paradigm, the signal is fixed in frequency and level, and the masker level required to bring the signal to threshold is measured as a function of masker frequency.

The authors note that these data and those of Figs. B27-0 and B29-0, show that the basic form of the psychophysical tuning curves remain rather constant at different signal levels. In general, the curves are narrowest at low sensation levels and at high signal frequencies. The frequency at which masking is most effective does not shift with changes in signal level, as demonstrated by a detailed analysis of the tuning curve shape at 1600 Hz (not plotted here).

Masker level at threshold plotted as a function of signal level is a linear function with a slope of 1.4.

Means: N=5.

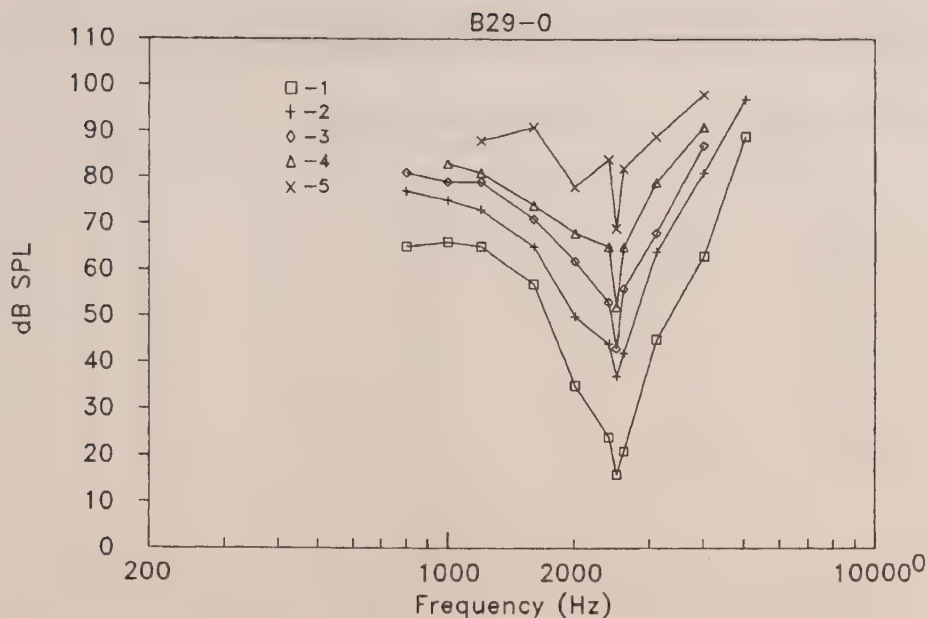


Fig. B29-0. The effect of signal level on psychophysical tuning curves at 2500 Hz for *Melopsittacus undulatus* (parakeet) (Saunders, Else, and Bock, 1978).

- 1- 10 dB SL signal level
- 2- 20 dB SL
- 3- 30 dB SL
- 4- 40 dB SL
- 5- 50 dB SL

Reference:

Saunders, J.C., Else, P.V., and Bock, G.R. (1978) Frequency selectivity in the parakeet (*Melopsittacus undulatus*) studied with psychophysical tuning curves. *J. Comp. Physiol. Psychol.* 92, 406-415.

Table B29-0. The effect of signal level on psychophysical tuning curves at 2500 Hz for *Melospittacus undulatus* (parakeet) (Saunders, Else, and Bock (1978).

Masker Frequency (Hz)	Masker Level at Threshold (dB SPL)				
	1	2	3	4	5
800	65	77	81		
1000	66	75	79	83	
1200	65	73	79	81	88
1600	57	65	71	74	91
2000	35	50	62	68	78
2400	24	44	53	65	84
2500	16	37	43	52	69
2600	21	42	56	65	82
3100	45	64	68	79	89
4000	63	81	87	91	98
5000	89	97			

Notes:

Instrumental shock avoidance conditioning using the descending method of limits psychophysical procedure. Maskers were continuous pure tones. Signals were pure tones with 50 msec rise/fall times. In this paradigm, the signal is fixed in frequency and level, and the masker level required to bring the signal to threshold is measured as a function of masker frequency.

The authors note that these data and those of Figs. B27-0 and B28-0, show that the basic form of the psychophysical tuning curves remain rather constant at different signal levels. In general, the curves are narrowest at low sensation levels and at high signal frequencies. The frequency at which masking is most effective does not shift with changes in signal level, as demonstrated by a detailed analysis of the tuning curve shape at 1600 Hz (not shown here).

Similar data on the effect of signal intensity on psychophysical tuning curves (not shown here) were presented by Saunders (1976).

Masker level at threshold plotted as a function of signal level is a linear function with a slope of 1.4.

Means: N=5.

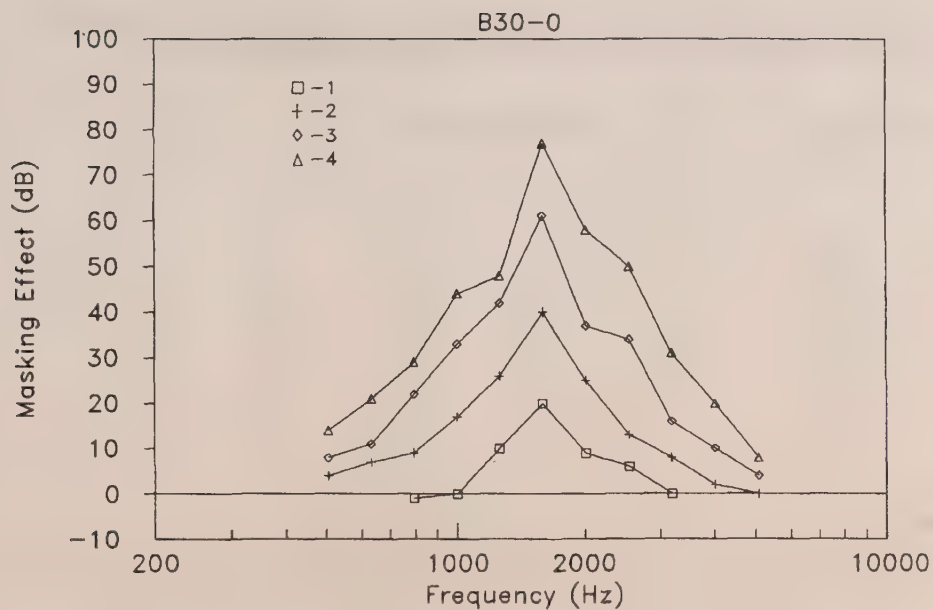


Fig. B30-0. The effect of a one-third octave noise band on tone detection in *Melopsittacus undulatus* (parakeet) (Saunders, Bock, and Farbach, 1978).

- 1- 26 dB sensation level (SL) masking noise band
- 2- 46 dB SL
- 3- 66 dB SL
- 4- 86 dB SL

Reference:

Saunders, J.C., Bock, G.R., and Farbach, S.E. (1978) Frequency selectivity in the parakeet (*Melopsittacus undulatus*) studied with narrow-band noise masking. *Sensory Processes* 2, 80-89.

Table B30-0. The effect of a one-third octave noise band on tone detection in *Melopsittacus undulatus* (parakeet) (Saunders, Bock, and Farbach, 1978).

Signal Frequency (Hz)	Threshold Shift (dB)			
	1	2	3	4
500		4	8	14
630		7	11	21
793	-1	9	22	29
1000	0	17	33	44
1260	10	26	42	48
1587	20	40	61	77
2000	9	25	37	58
2520	6	13	34	50
3175	0	8	16	31
4000		2	10	20
5040		0	4	8

Notes:

Instrumental shock avoidance conditioning using the descending method of limits. The masker was a continuous 1/3 octave noise band centered at 1600 Hz, and presented at the sensation levels indicated. Signals were pure tones with 50 msec rise/fall times.

The authors point out that the threshold shift function of masker level is linear with a slope of approximately 1.0 for the 1600 Hz signal (in the center of the masker band). The functions for the 1250 and 2500 Hz signals are linear but with lower slopes of about 0.68 and 0.79, respectively. This means that the filter function becomes sharper at the higher masker levels. The Q_{10dB} values range from 2.13 at 26 dB SL, to 3.26 at 86 dB SL.

Means: N=5.

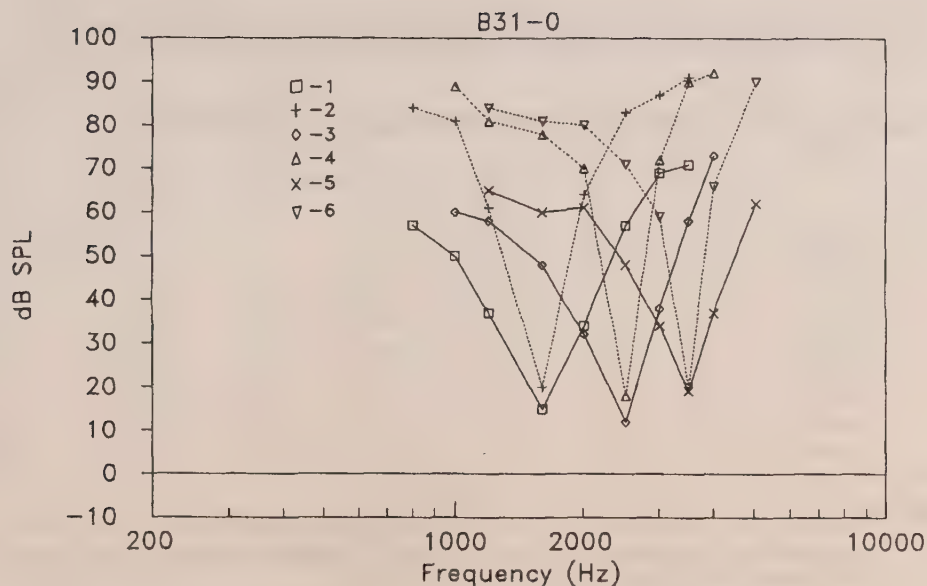


Fig. B31-0. Psychophysical tuning curves for *Melopsittacus undulatus* (parakeet) determined in simultaneous and forward masking (Kuhn and Saunders, 1980).

The dashed lines indicate forward masking conditions.

- 1- 1600 Hz signal, simultaneous masking
- 2- 1600 Hz signal, forward masking
- 3- 2500 Hz signal, simultaneous masking
- 4- 2500 Hz signal, forward masking
- 5- 3500 Hz signal, simultaneous masking
- 6- 3500 Hz signal, forward masking

Reference:

Kuhn, A., and Saunders, J.C. (1980) Psychophysical tuning curves in the parakeet: A comparison between simultaneous and forward masking procedures. *J. Acoust. Soc. Amer.* 68, 1892-1894.

Table B31-0. Psychophysical tuning curves for *Melopsittacus undulatus* (parakeet) determined in simultaneous and forward masking (Kuhn and Saunders, 1980).

Masker Frequency (Hz)	Masker Level at Signal Detection Threshold (dB SPL)					
	1	2	3	4	5	6
800	57	84				
1000	50	81	60	89		
1200	37	61	58	81	65	84
1600	15	20	48	78	60	81
2000	34	64	32	70	61	80
2500	57	83	12	18	48	71
3000	69	87	38	72	34	59
3500	71	91	58	90	19	20
4000			73	92	37	66
5000					62	90

Notes:

Instrumental shock avoidance conditioning using the descending method of limits.

In simultaneous masking, tonal maskers were presented continuously. Tone signals were presented at 10 dB SL with 50 msec rise/fall times.

In forward masking, tonal maskers were pulsed (280 msec in duration, 15 msec linear rise/fall times, separated by 450 msec). Signals of 50 msec duration and 18 msec rise/fall times followed the maskers with no delay and no temporal overlap.

Means: N=4.

More sharply tuned psychophysical tuning curves in forward masking than in simultaneous masking has also been observed in most mammals and humans, but not consistently observed in fish.

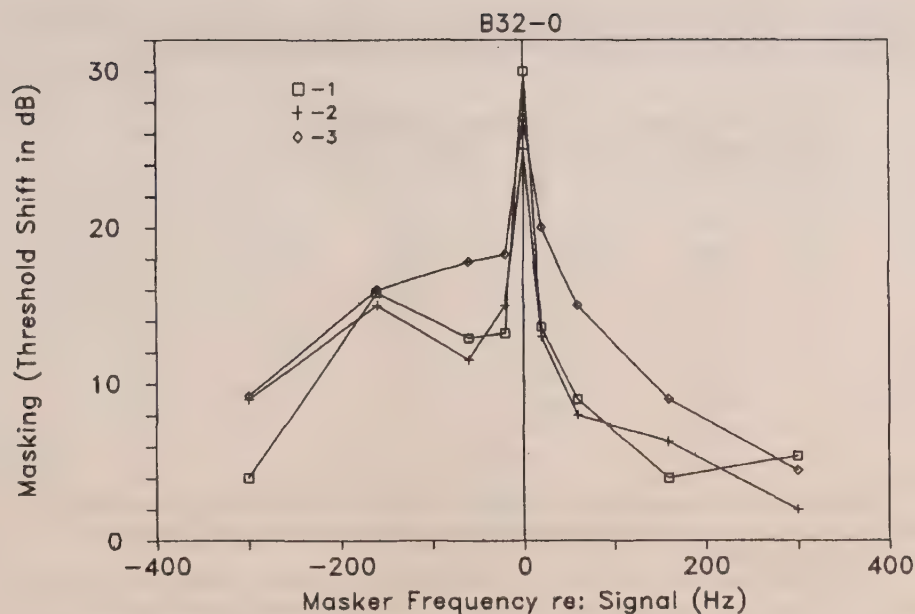


Fig. B32-0. Tone-on-tone masking functions for *Melopsittacus undulatus* (parakeet) determined in backward, forward, and combined forward-backward masking.

- 1- Backward masking
- 2- Combined backward-forward masking
- 3- Forward masking

Reference:

Dooling, R.J., and Searcy, M.H. (1985) Nonsimultaneous auditory masking in the budgerigar (*Melopsittacus undulatus*). *J. Comp. Psychol.* 99, 226-230.

Table B32-0. Tone-on-tone masking functions for *Melopsittacus undulatus* (parakeet) determined in backward, forward, and combined forward-backward masking.

Masker Frequency (Hz re: probe)	Amount of Masking (dB)		
	1	2	3
-300	4	9	9.2
-160	15.8	15	16
-60	12.9	11.5	17.8
-20	13.2	15	18.3
0	30	25	27
20	13.6	13	20
60	9	8	15
160	4	6.3	9
300	5.4	2	4.5

Notes:

Instrumental shock avoidance conditioning using a modified method of limits psychophysical procedure. Animals trained to avoid shock during signal presentation by biting a bar. Means: N=3.

Probe tones had 7 msec duration (at full amplitude), 4 msec rise/fall times, and a frequency fixed at 2.86 kHz. Maskers were tones of 100 msec with 5 msec rise/fall times, fixed in intensity at 60 dB SPL. Maskers were always presented as an identical pair of tone bursts, separated by 17 msec, repeated once per sec. Time separation between maskers and signal was zero msec.

In the backward masking case, the probe tone preceded the masker tone pair. In combined backward-forward masking, the signal was presented between the pair. For forward masking, the signal followed the second masker of the pair.

It is interesting to note in this case that the forward masker is the most effective one, and is even more effective than combined forward-backward masking. This suggests that the two forward masker bursts may summate over their combined duration (217 msec) in their masking effects.

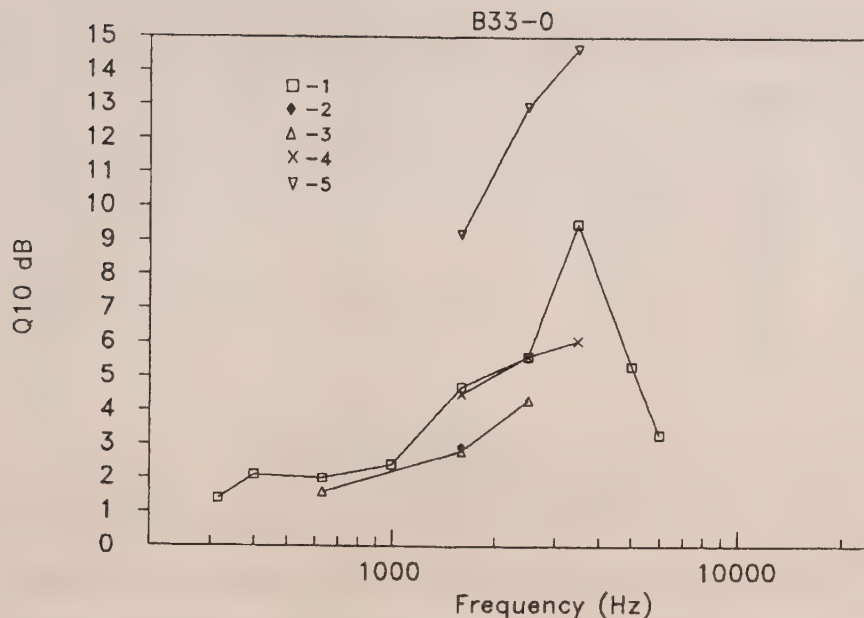


Fig. B33-0. Q_{10dB} values for psychophysical tuning curves and other masking functions in *Melopsittacus undulatus* (parakeet).

- 1- Saunders, Rintelmann, and Bock (1979)
- 2- Saunders, Bock, and Fahrbach (1978)
- 3- Saunders and Else (1976)
- 4- Kuhn and Saunders (1980) - simultaneous masking
- 5- Kuhn and Saunders (1980) - forward masking

References:

- Kuhn, A., and Saunders, J.C. (1980) Psychophysical tuning curves in the parakeet: A comparison between simultaneous and forward masking procedures. *J. Acoust. Soc. Amer.* 68, 1892-1894.
- Saunders, J.C., Bock, G.R., and Farbach, S.E. (1978) Frequency selectivity in the parakeet (*Melopsittacus undulatus*) studied with narrow-band noise masking. *Sensory Processes* 2, 80-89.
- Saunders, J.C., and Else, P.V. (1976) Pure tone masking in the parakeet: A preliminary report. *Trans. Amer. Acad. Opthal. Oto.* 82, 356-362.
- Saunders, J.C., Rintelmann, W.F., and Bock, G.R. (1979) Frequency selectivity in bird and man: A comparison among critical ratios, critical bands and psychophysical tuning curves. *Hear. Res.* 1, 303-323.

Table B33-0. Q_{10dB} values for psychophysical tuning curves and other masking functions in *Melospittacus undulatus* (parakeet).

Frequency (Hz)	1	2	Q_{10dB} 3	4	5
315	1.4				
400	2.1				
630	2		1.6		
1000	2.4				
1600	4.7	2.88	2.8	4.49	9.18
2500	5.6		4.3	5.6	12.95
3500	9.5			6.06	14.66
5000	5.3				
6000	3.3				

Notes:

All studies based on instrumental shock avoidance conditioning using the descending method of limits psychophysical procedure.

Q_{10dB} is a measure of the selectivity of a filter defined as the center frequency of the filter function divided by the bandwidth (in Hz) 10 dB above the point of best sensitivity.

All the data shown here are derived from the filter functions from the following

Figures:

- 1- B23-0 - simultaneous psychophysical tuning curves, tone maskers, tone signals
- 2- B30-0 - simultaneous masking of tones by fixed narrowband noise
- 3- B24-0 - simultaneous masking of tones by fixed tone maskers
- 4- B31-0 - simultaneous psychophysical tuning curves, tone maskers, tone signals
- 5- B31-0 - forward masked psychophysical tuning curves, tone maskers, tone signals

See the Notes for the individual figures.

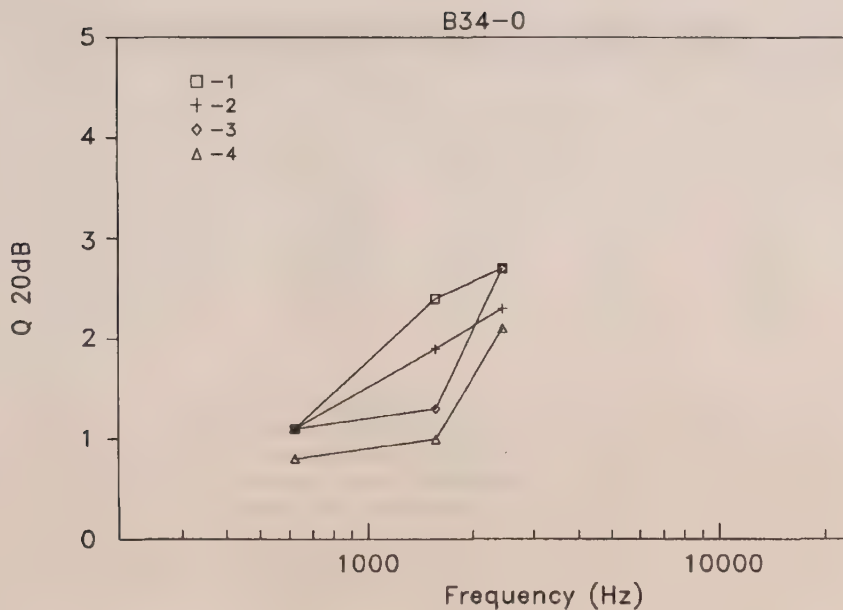


Fig. B34-0. Q_{20dB} values for psychophysical tuning curves in *Melopsittacus undulatus* (parakeet) for signals of different frequency and level (Saunders, Else, and Bock, 1978).

- 1- 10 dB sensation level (SL) signal
- 2- 20 dB SL
- 3- 30 dB SL
- 4- 40 dB SL

Reference:

Saunders, J.C., Else, P.V., and Bock, G.R. (1978) Frequency selectivity in the parakeet (*Melopsittacus undulatus*) studied with psychophysical tuning curves. J. Comp. Physiol. Psychol. 92, 406-415.

Table B34-0. Q_{20dB} values for psychophysical tuning curves in *Melopsittacus undulatus* (parakeet) for signals of different frequency and level (Saunders, Else, and Bock, 1978).

Frequency (Hz)	Q_{20dB}			
	1	2	3	4
630	1.1	1.1	1.1	0.8
1600	2.4	1.9	1.3	1
2500	2.7	2.3	2.7	2.1

Notes:

See Notes for Figs. B26-0 to B29-0 for the origins of these data.

Note that these values are Q_{20dB} , meaning that the filter center frequency is divided by the bandwidth 20 dB above the sound level at best sensitivity. The authors chose this measure so that the above comparison would not show the effects of the very sharp tip sometimes observed on the psychophysical tuning curves for the parakeet (e.g. B26-0 through B28-0).

These data indicate that frequency selectivity of the parakeet auditory system is more acute at the higher frequencies, and for low level signals. Intense signals give broader tuning estimates than weak signals.

Means: N= 4 to 7.

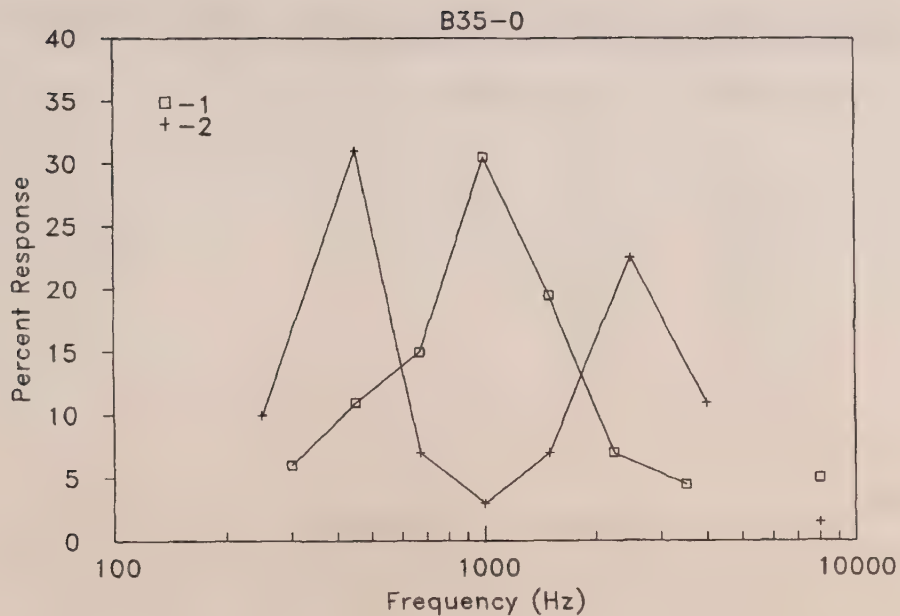


Fig. B35-0. Stimulus generalization along the dimension of pure tone frequency in *Columba livia* (pigeon) (Jenkins and Harrison, 1960).

- 1- 1000 Hz training frequency
- 2- 450 Hz and 2500 Hz training frequencies

Reference:

Jenkins, H.M., and Harrison, R.H. (1960) Effect of discrimination training on auditory generalization. *J. Exp. Psychol.* 59, 246-253.

Table B35-0. Stimulus generalization along the dimension of pure tone frequency in *Columba livia* (pigeon) (Jenkins and Harrison, 1960).

Test Frequency (Hz)	Percent Response	
	1	2
250		10
300	6	
450	11	31
670	15	7
1000	30.5	3
1500	19.5	7
2250	7	
2500		22.5
3500	4.5	
4000		11
No Signal	5	1.5

Notes:

Operant conditioning (key peck) for a food reward. Animals were rewarded for pecking a key in the presence of an auditory signal, and not rewarded for pecking when no signal was presented. Signals were 70 dB SPL tone bursts (750 msec on, and 250 msec off, repeating for 33 sec). Generalization measurements were made by presenting tone frequencies other than the training frequencies, and measuring the key peck response in their presence. The unconnected points indicate the level of response in the "no tone" condition.

1- With the training frequency at 1000 Hz, test tone frequencies higher or lower were not as effective in evoking responses as the training frequency. There is a monotonic decline in response as the test frequency deviates from 1000 Hz. This demonstrates that the dimension of tone frequency comes to control behavior in this situation, and that there is a perceptual dimension (perhaps like pitch) that is monotonic with tone frequency.

2- With training frequencies of 450 and 2500 Hz, both come to control behavior independently.

The data from stimulus generalization experiments are useful in determining the relations between dimensions of sound stimuli and dimensions of perceptual response.

Generalization functions are relatively flat when animals are not first trained to discriminate between two stimulus conditions (such as between the presence and absence of a tone signal).

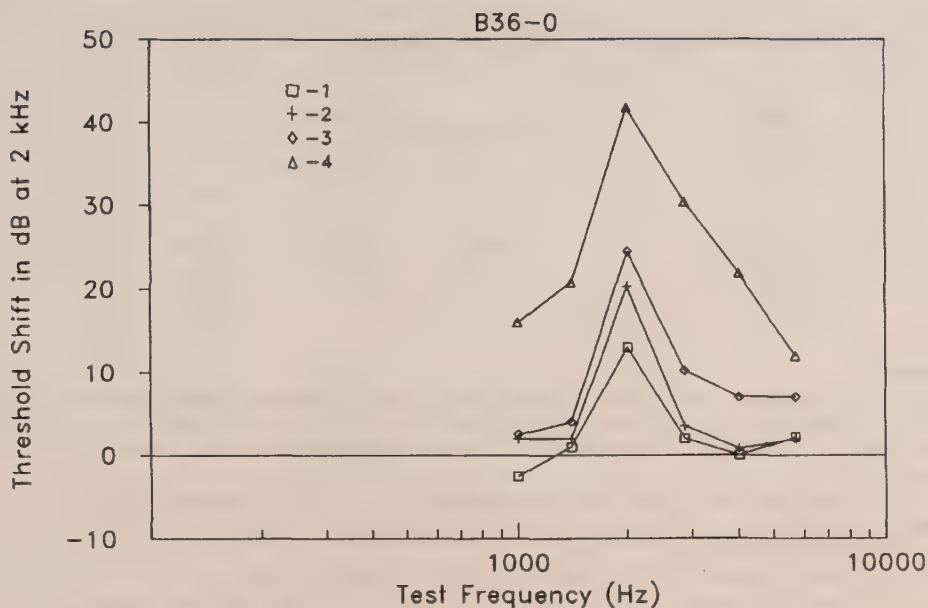


Fig. B36-0. Frequency dependent threshold shift caused by exposure to four different noise intensities in *Melopsittacus undulatus* (parakeet).

- 1- 76 dB SPL noise exposure, Dooling and Saunders, 1974
- 2- 86 dB SPL noise exposure, Saunders and Dooling, 1974
- 3- 96 dB SPL noise exposure, Saunders and Dooling, 1974
- 4- 106 dB SPL noise exposure, Dooling and Saunders, 1974

Reference:

- Dooling, R.J., and Saunders, J.C. (1974) Threshold shift produced by continuous noise exposure in the parakeet (*Melopsittacus undulatus*). *J. Acoust. Soc. Amer.* 55, S77(A). Cited by Dooling, R.J. (1980) Behavior and psychophysics of hearing in birds. In A. N. Popper and R.R. Fay (eds), *Comparative studies of Hearing in Vertebrates*. Springer-Verlag: New York, pp. 261-288.
- Saunders, J., and Dooling, R.J. (1974) Noise-induced threshold shift in the parakeet (*Melopsittacus undulatus*). *Proc. Nat. Acad. Sci. USA* 71, 1962-1965.

Table B36-0. Frequency dependent threshold shift caused by exposure to four different noise intensities in *Melopsittacus undulatus* (parakeet).

Test Frequency (Hz)	Asymptotic Threshold Shift (dB)			
	1	2	3	4
2000	13	20.3	24.5	41.8
2860	2	3.5	10.2	30.4
4000	0	0.8	7	21.9
5700	2.2	2	7	12

Notes:

Instrumental shock avoidance conditioning using a modified *descending* method of limits. Restrained animals were trained to avoid shock during the presentation of a tone signal by biting a bar. Means: N=4 16-week old animals, surgically deafened in the left ear.

Signal was one four sec tone presentation at the indicated frequencies, with 50 msec rise/fall times. Noise was 1/3 octave band centered at 2 kHz presented in a reverberation chamber.

These threshold shifts illustrate the degree of frequency selectivity of the parakeet ear. This pattern of threshold shift is more symmetrical than that normally observed in mammals.

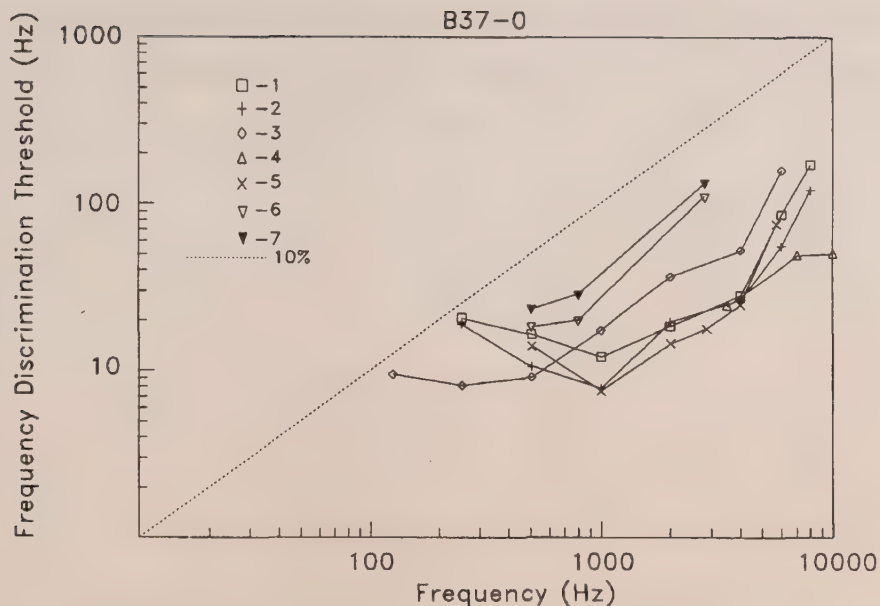


Fig. B37-0. Frequency discrimination thresholds for several bird species.

- 1- *Agelaius phoeniceus* - redwing blackbird (Sinnott, Sachs, and Hienz, 1980)
- 2- *Molothrus ater* - brown-headed cowbird (Sinnott, Sachs, and Hienz, 1980)
- 3- *Columba livia* - homing pigeon (Sinnott, Sachs, and Hienz, 1980)
- 4- *Tyto alba* - barn owl (Quine and Konishi, 1974)
- 5- *Melopsittacus undulatus* - parakeet (Dooling and Saunders, 1975)
- 6- *Gallus gallus* - 4-day old chicken (Gray and Rubel, 1985)
- 7- *Gallus gallus* - 0-day old chicken (Gray and Rubel, 1985)

References:

- Dooling, R.J., and Saunders, J.C. (1975) Hearing in the parakeet (*Melopsittacus undulatus*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations. *J. Comp. Physiol. Psychol.* 88, 1-20.
- Gray, L., and Rubel, E.W. (1987) Development of auditory thresholds and frequency difference limens in chickens. In G. Gottlieb and N. Krasnegor (eds), *Measurement of Audition and Vision in the First Year of Postnatal Life: A Methodological Overview*. Ablex: Norwood, NJ, pp. 145-165.
- Quine, D.B., and Konishi, M. (1974) Absolute frequency discrimination in the barn owl. *J. Comp. Physiol.* 93, 347- 360.
- Sinnott, J.M., Sachs, M.B., and Hienz, R.D. (1980) Aspects of frequency discrimination in passerine birds and pigeons. *J. Comp. Physiol. Psychol.* 94, 401-415.

Table B37-0. Frequency discrimination thresholds for several bird species.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)						
	1	2	3	4	5	6	7
125			9.45				
250	20.5	18.9	8.1				
500	16.4	10.5	9.07		13.9	18	23
800						19.5	28
1000	12	7.77	17.3		7.5		
2000	18.4	19.4	36.4		14.5		
2800						108	131
2860					17.7		
3500				24.5			
4000	27.9	25.8	52.5		24.7		
5700					75.2		
6000	85.9	55.4	159				
7000				49			
8000	171	120					
10000				50			

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli (go, no-go). Means: N=7.

A constant background stimulus consisting of tone bursts (250 msec on, 250 msec off, 20 msec rise/fall times) at the "standard" frequency was presented. The signal consisted of a period during which the frequency of the bursts alternated between the standard and a comparison (higher) frequency.

2- Same as #1. Means: N=7.

3- Same as #1. Means: N=2.

4- Animals differentially trained to fly from a perch for a food reward upon the presentation of a tone signal of a particular frequency. Presentations of a "positive" frequency were reinforced while presentations of any other tone frequency were not. This is referred to by the authors as "absolute" frequency discrimination requiring memory of the "positive" frequency. Thresholds were the smallest frequency differences that could be discriminated with a probability ≤ 0.05 . Signals at 30 dB sensation level (50 msec rise/fall times). Means: N=2.

5- Instrumental shock avoidance conditioning using the method of limits psychophysical procedure. A restrained bird was trained to bite a rod upon the presentation of a tone in order to avoid shock. Means: N=6.

A background stimulus (tone bursts 100 msec on, 400 msec off, 20 msec rise/fall times) at the "standard" frequency was presented. The signal was an alternation between the standard and comparison (upward shift) frequency at 60 dB sensation level.

6- Unconditioned peep-suppression method using an adaptive tracking procedure (see Notes for Fig. B9-0). The signal consisted of an increment of the frequency of a background tone. Birds tested on the 4th day after hatching.

7- Same as #6. Birds tested on the day of hatching.

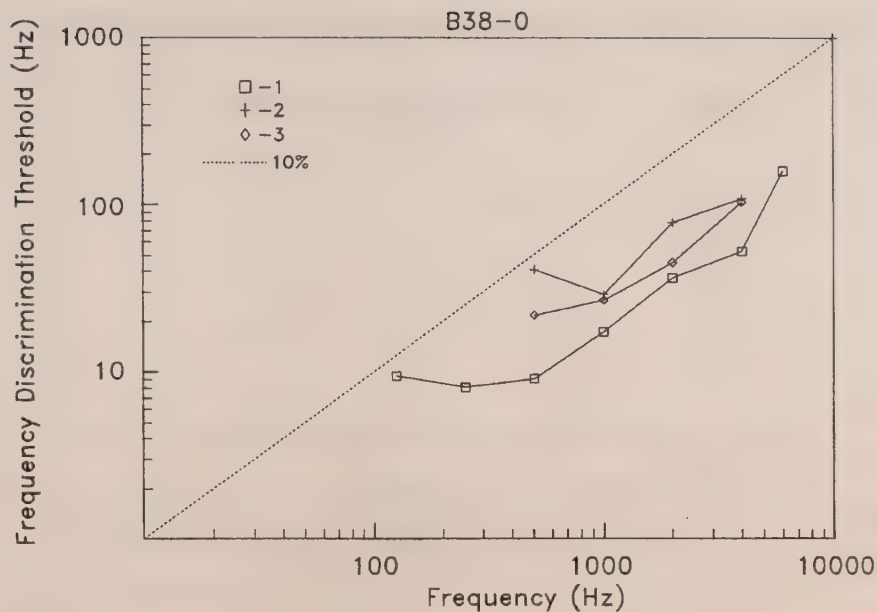


Fig. B38-0. Frequency discrimination thresholds for *Columba livia* (pigeon).

- 1- Sinnott, Sachs, and Hienz, 1980
- 2- Delius and Tarpey, 1974
- 3- Price, Dalton, and Smith, 1967

References:

- Delius, J.D., and Tarpey, R.M. (1974) Stimulus control of heart rate by auditory frequency and auditory pattern in pigeons. *J. Exp. Anal. Behav.* 21, 297-306.
- Price, L.L., Dalton, L.W. Jr., and Smith, J.C. (1967) Frequency DL in the pigeon as determined by conditioned suppression. *J. Aud. Res.* 7, 229-239.
- Sinnott, J.M., Sachs, M.B., and Hienz, R.D. (1980) Aspects of frequency discrimination in passerine birds and pigeons. *J. Comp. Physiol. Psychol.* 94, 401-415.

Table B38-0. Frequency discrimination thresholds for *Columba livia* (pigeon).

Frequency (Hz)	Frequency Discrimination Threshold (Hz)		
	1	2	3
125	9.45		
250	8.1		
500	9.07	43	21.7
1000	17.3	29	26.7
2000	36.4	79	45
4000	52.5	100	103.3
6000	159		

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli (go, no-go). Means: N=7

A constant background stimulus consisting of tone bursts (250 msec on, 250 msec off, 20 msec rise/fall times) at the "standard" frequency was presented. The signal consisted of a period during which the frequency of the bursts alternated between the standard and a comparison (higher) frequency. Means: N=2.

2- Classical conditioning of heart rate (tachycardia) using electric shock as the unconditioned stimulus. The method of constant stimuli was used. In each experimental session, animals were given 40 blocks of six trials. The first five trials were 10 sec presentations of the "standard" tone frequency, without shock. The sixth trial was a "comparison" tone of different frequency, followed by shock. Threshold defined as the difference in frequency between the standard and comparison frequencies in which a heart rate increase was found on 75% of the trials.

Signals were 10 sec duration tones at 75 dB SPL. Means: N=2.

3- Classically conditioned suppression of an operantly reinforced key-peck for food using a descending method of limits. Background tone pulses (200 msec duration, 200 msec off) were caused to alternate in frequency for 20 sec, signalling shock. 50 dB sensation level. Means: N=3.

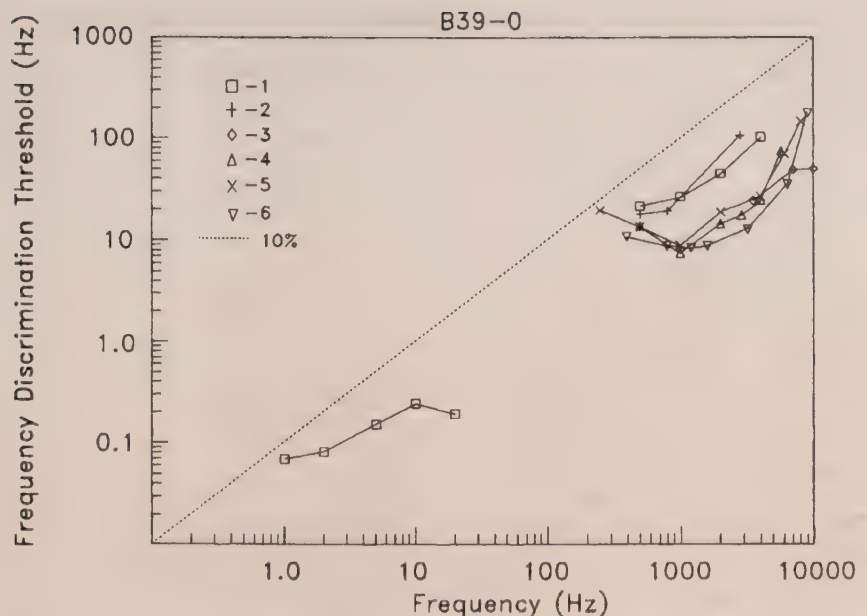


Fig. B39-0. Frequency discrimination thresholds for several bird species (summary).

- 1- *Columba livia* - pigeon
1-20 Hz (Quine and Kreithen, 1981)
500-4000 Hz (Median pigeon from Fig. B38-0)
- 2- *Gallus domesticus* - chicken, 4-day old, Fig. B37-0
- 3- *Tyto alba* - barn owl, Fig. B37-0
- 4- *Melopsittacus undulatus* - parakeet, Fig. B37-0
- 5- *Agelaius phoeniceus* and *Molothrus ater* - blackbirds, Fig. 37-0
- 6- *Sturnus vulgaris* - European starling (Kuhn, Leppelsack, and Schwartzkopff, 1980)

References:

- Kuhn, A., Leppelsack, H.J., and Schwartzkopff, J. (1980) Measurement of frequency discrimination in the starling (*Sturnus vulgaris*) by conditioning of heart rate. *Naturwissenschaften* 67, 102.
- Quine, D.B., and Kreithen, M.L. (1981) Frequency shift discrimination: Can homing pigeons locate infrasounds by doppler shifts? *J. Comp. Physiol.* 141, 153-155.

Table B39-0. Frequency discrimination thresholds for several bird species (summary).

Frequency (Hz)	Frequency Discrimination Threshold (Hz)					
	1	2	3	4	5	6
1	0.068					
2	0.08					
5	0.15					
10	0.24					
20	0.19					
250					19.7	
500	21.7	8		13.9	13.5	
400						10.8
800		19.5				8.8
1000	26.7			7.5	8.9	
1200						8.4
1600						8.8
2000	45			14.5	18.9	
2800		108				
2860				17.7		
3200						12.8
3500			24.5			
4000	103.3			24.7	26.9	
5700				75.2		
6000					70.7	
6400						35.2
7000			49			
8000					146	
9000						175.5
10000			50			

Notes:

1- For frequencies from 1-20 Hz, classical cardiac conditioning (bradycardia) with a shock UCS was used with the method of constant stimuli. See Notes for Fig. B5-0 and B62-0 for more details on the method. The background consisted of a continuous pure tone at 30 dB sensation level. The signal was smoothly shifted upward in frequency within 800 msec.

The rationale for this experiment was to demonstrate the possibility that pigeons could orient to the source of low frequency sounds by determining the direction and degree of Doppler shifts caused by their own change in velocity (turning). A pigeon turns 90° in flight in about 800 msec.

Control tests were conducted in which the amplitude and frequency of the background tone was varied. Amplitude shifts from -12 to +4 dB had no effect on frequency discrimination. For frequencies from 500 to 4000 Hz, data are median thresholds for pigeon from the data shown in Fig. B38-0.

5- Thresholds for the two blackbirds in Fig. B37-0 are averaged here.

6- See Notes for Fig. B4-0, #1. Background stimulus tone bursts 1 sec duration, repeated once/4 sec, 60 dB sensation level. Means: N=6.

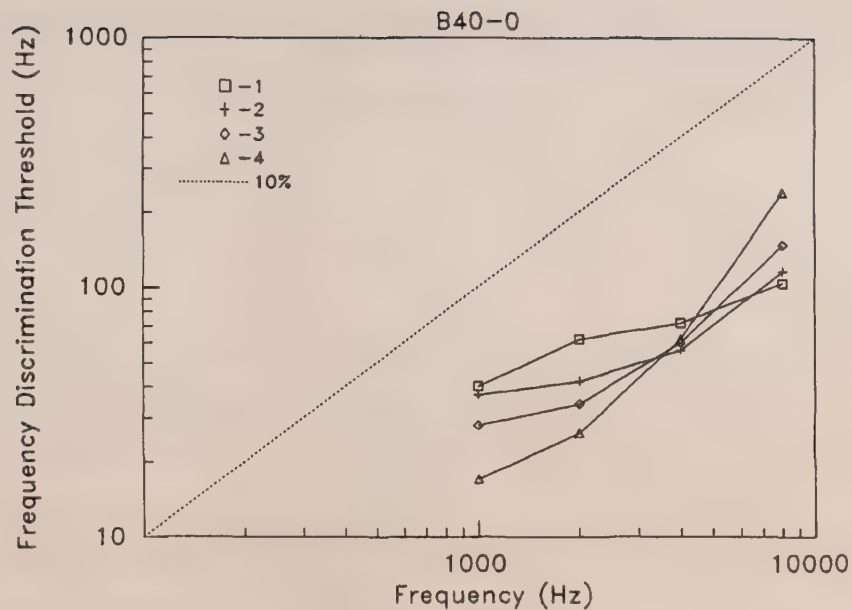


Fig. B40-0. Frequency discrimination thresholds for *Agelaius phoeniceus* and *Molothrus ater* (blackbirds) at four different sensation levels (Sinnott, Sachs, and Hienz, 1980).

- 1- 10 dB sensation level
- 2- 20 dB
- 3- 30 dB
- 4- 40 dB

Reference:

Sinnott, J.M., Sachs, M.B., and Hienz, R.D. (1980) Aspects of frequency discrimination in passerine birds and pigeons. *J. Comp. Physiol. Psychol.* 94, 401-415.

Table B40-0. Frequency discrimination thresholds for *Agelaius phoeniceus* and *Molothrus ater* (blackbirds) at four different sensation levels.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)			
	1	2	3	4
1000	40	37	28	17
2000	62	42	34	26
4000	72	56	60	62
8000	104	116	148	240

Notes:

Operant conditioning for a food reward using the method of constant stimuli (go, no-go). Three redwings and five cowbirds.

A constant background stimulus consisting of tone bursts (250 msec on, 250 msec off, 20 msec rise/fall times) at the "standard" frequency was presented. The signal consisted of a period during which the frequency of the bursts alternated between the standard and a comparison (higher) frequency.

Note that increasing sensation level causes a loss of frequency discrimination acuity at the high frequencies, and a gain in acuity at low frequencies. This suggests a different mechanism for frequency discrimination at low and high frequencies.

This experiment also tested the effect on the frequency discrimination threshold of the direction of the frequency transitions during the signal (comparison frequency above or below the standard frequency). At 2 kHz, thresholds are lower for upward shifts, but at 8 kHz, thresholds are lower for downward shifts.

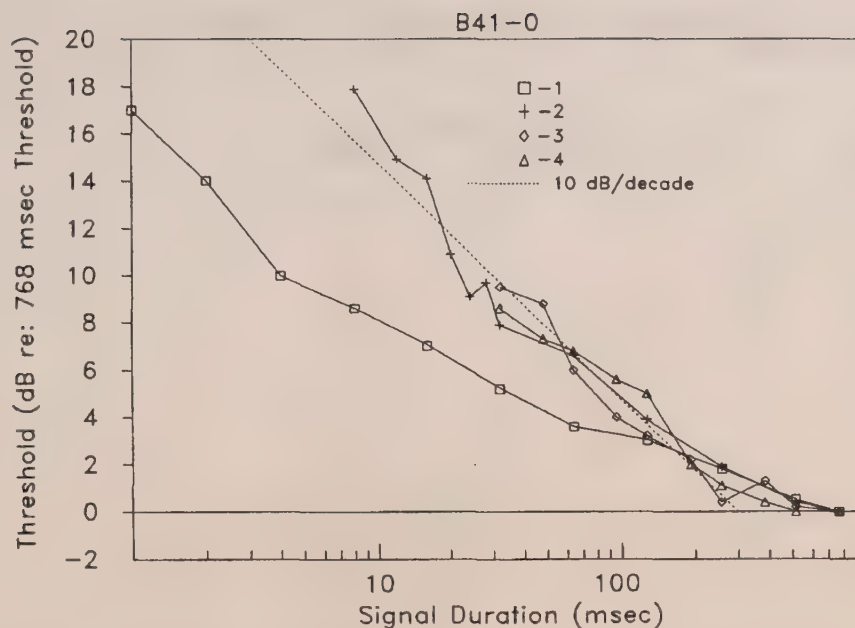


Fig. B41-0. Signal detection threshold as a function of signal duration in parakeet and field sparrow.

- 1- *Melopsittacus undulatus* - parakeet, noise signal (Dooling and Searcy, 1985)
- 2- *Melopsittacus undulatus* - parakeet, 2.86 kHz tone, (Dooling and Searcy, 1985)
- 3- *Melopsittacus undulatus* - parakeet, 2.86 kHz tone (Dooling, 1979)
- 4- *Spizella pusilla* - field sparrow, 2.86 kHz tone (Dooling, 1979)

References:

- Dooling, R.J. (1979) Temporal summation of pure tones in birds. *J. Acoust. Soc. Amer.* 65, 1058-1060.
- Dooling, R.J., and Searcy, M.H. (1985) Temporal integration of acoustic signals by the budgerigar. *J. Acoust. Soc. Amer.* 77, 1917-1920.

Table B41-0. Signal detection threshold as a function of signal duration in parakeet and field sparrow.

Signal Duration (msec)	Signal Threshold (dB re: Threshold at 768 msec)			
	1	2	3	4
1	17			
2	14			
4	10			
8	8.6	17.9		
12		14.9		
16	7	14.1		
20		10.9		
24		9.1		
28		9.7		
32	5.2	7.9	9.5	8.6
48			8.8	7.3
64	3.6	6.7	6	6.8
96			4	5.6
128	3	3.9	3.2	5
192			2.2	2
256	1.8	1.9	0.4	1.1
384			1.3	0.4
512	0.5	0.4	0.2	0
768	0	0	0	0

Notes:

1-2- Instrumental shock avoidance using a modified method of constant stimuli. A restrained animal was trained to bite a bar to avoid shock in the presence of a tone. All signals presented against a broad band noise background at -10 dB SPL spectrum level. Rise/fall times were 1 and 4 msec for the noise and tone, respectively. Means: N=6.

The authors fitted both the noise and tone data with two functions, one at short durations, and another at long durations. For noise, the segment between 4 and 768 msec has a slope of -1.5 dB per doubling of duration. For tones, the segment between 32 and 768 msec has a slope of -2.5 dB per doubling of duration. These values correspond to power function exponents of -0.53 and -0.61, respectively. The authors determined that the time constant for tones at durations greater than 16 msec is about 230 msec using the definition of Plomp and Bouman, 1959.

3-4- Same methods as in #1 and #2, except that animals were tested in quiet using 5 msec rise/fall times. The author determined that the time constant for these two species is about 230 msec using the definition of Plomp and Bouman, 1959.

3- Means: N=2

4- Means: N=2

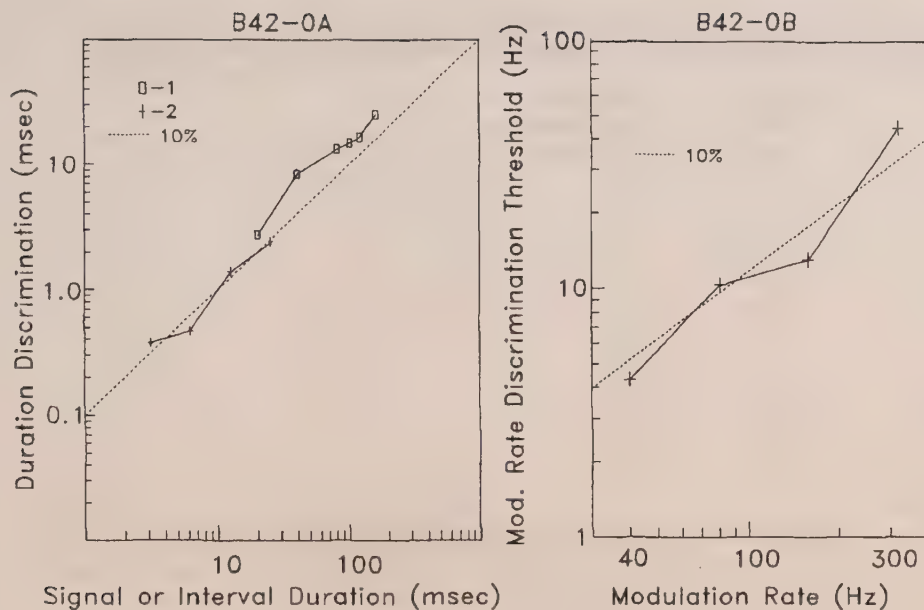


Fig. B42-0. A. Just-discriminable change in signal duration or repetition interval as a function of signal duration or interval. B. Modulation rate discrimination threshold (in Hz) as a function of modulation rate (in Hz). *Melopsittacus undulatus* (parakeet)

- 1- 2.86 kHz tone, duration discrimination (Dooling and Haskell, 1978)
- 2- Amplitude-modulated noise, modulation period discrimination (Dooling and Searcy, 1981)

References:

- Dooling, R.J., and Haskell, R.J. (1987) Auditory duration discrimination in the parakeet (*Melopsittacus undulatus*). *J. Acoust. Soc. Amer.* 63, 1640-1642.
- Dooling, R.J., and Searcy, M.H. (1981) Amplitude modulation thresholds for the parakeet (*Melopsittacus undulatus*). *J. Comp. Physiol.* 143, 383-388.

Table B42-0A. Just-discriminable change in signal duration or repetition interval as a function of signal duration or interval in *Melopsittacus undulatus* (parakeet).

Signal Duration (msec)	Duration Discrimination Threshold	
	1	2
3.125		0.376
6.25		0.470
12.5		1.414
20	2.75	
25		2.427
40	8.4	
80	13.32	
100	14.9	
120	16.62	
160	25.2	

Notes:

1- Instrumental shock avoidance using a modified method of limits. Restrained animals were trained to bite a bar to avoid shock in the presence of a change in sound-burst duration. Background stimulus consisted of tone bursts at 60 dB sensation level, with 5 msec rise/fall times, repeated once per 400 msec. Animals discriminated a change in tone burst duration. Means: N=2.

2- Instrumental shock avoidance using a modified method of limits. Restrained animals were trained to bite a bar to avoid shock in the presence of a change in amplitude modulation period. Background stimulus consisted of continuous sinusoidally amplitude modulated noise with an overall intensity of from 40 to 70 dB SPL. Animals discriminated a change in envelope repetition period. Means: N=3.

Table B42-0B. Modulation rate discrimination threshold as a function of modulation rate in *Melopsittacus undulatus* (parakeet).

Modulation Rate (Hz)	Modulation Rate Discrimination Threshold (Hz)
40	4.3
80	10.2
160	13
320	43.7

Notes:

These are the data from #2 in Fig. B42-0A above, recalculated as modulation rate discrimination thresholds. The dashed line indicates a 10% threshold.

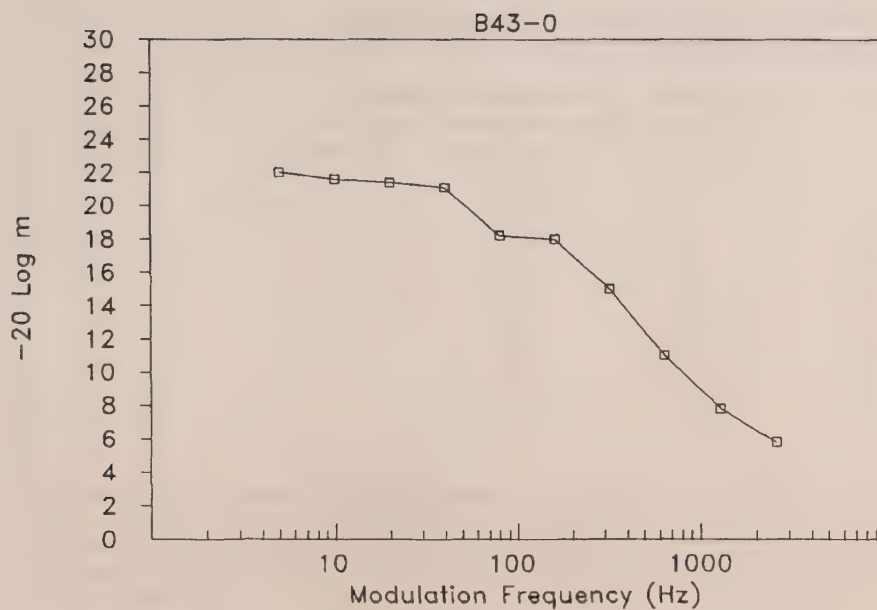


Fig. B43-0. Temporal Modulation Transfer Function for *Melopsittacus undulatus* (parakeet) (Dooling and Searcy, 1981).

Reference:

Dooling, R.J., and Searcy, M.H. (1981) Amplitude modulation thresholds for the parakeet (*Melopsittacus undulatus*). J. Comp. Physiol. 143, 383-388.

Table B43-0. Temporal Modulation Transfer Function for *Melopsittacus undulatus* (parakeet) (Dooling and Searcy, 1981).

Modulation Rate (Hz)	Just-Detectable Amount of Amplitude Modulation (m) (-20 Log m)
5	22
10	21.6
20	21.4
40	21.1
80	18.2
160	18
320	15
640	11
1280	7.8
2560	5.8

Notes:

The temporal modulation transfer function (TMTF) describes how the minimum detectable depth of sinusoidal amplitude modulation (SAM) varies as a function of modulation frequency. The TMTF provides a systematic description of the sensitivity with which the auditory system detects temporal envelope patterns, and can be thought of as the frequency response function of an envelope detector. The waveform carrier that is amplitude-modulated is usually noise, since the process of modulation produces no changes in the long-term amplitude spectrum of the noise carrier signal. Thus, detection of SAM on a noise carrier is not mediated by a spectral cue.

This TMTF has the characteristics of a low-pass filter. The frequency at which sensitivity falls from a maximum by 3 dB is about 92 Hz, and the equivalent time constant ($1/(2 \times \pi \times f)$, where f is the 3 dB-down frequency) is 1.7 msec.

The degree of amplitude modulation is measured as the index of modulation (m). The value m is equal to $(P-T)/(P+T)$, where P is the sound pressure at an envelope maximum, and T is the pressure at an envelope trough, or minimum. Modulation thresholds can be recalculated as intensity difference thresholds (in dB) as $20 \text{ Log } (P/T)$.

Instrumental shock avoidance using a modified method of limits. Restrained animals were trained to bite a bar to avoid shock in the presence of amplitude modulation impressed on an otherwise flat-envelope noise carrier. Means: N=5.

Temporal resolving power of the auditory system has also been characterized by the gap detection threshold. This is defined as the shortest gap of silence occurring during continuous broad band noise that is detectable. Dooling, Zoloth and Baylis (1978) determined the gap detection threshold of the house finch (*Carpodacus mexicanus*) to be 4.45 msec (average of two animals trained and tested using an instrumental shock avoidance paradigm).

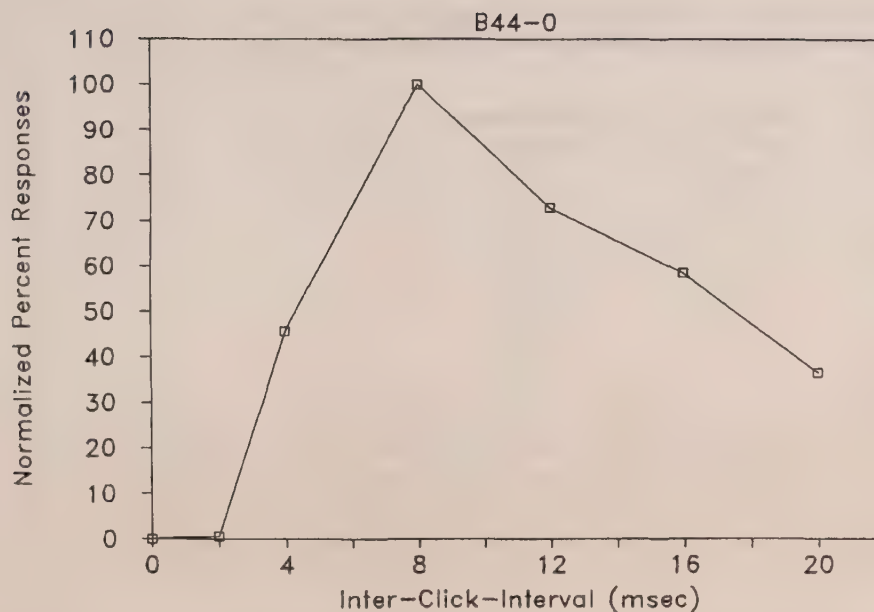


Fig. B44-0. Time resolution of clicks in *Pyrrhula pyrrhula* (bullfinch) studied with a stimulus generalization paradigm (Wilkinson and Howse, 1975).

Reference:

Wilkinson, R., and Howse, P.E. (1975) Time resolution of acoustic signals by birds.
Nature, 258, 320-321.

Table B44-0. Time resolution of clicks in *Pyrrhula pyrrhula* (bullfinch) studied with a stimulus generalization paradigm (Wilkinson and Howse, 1975).

Inter-Click Interval (msec)	Percent Responses (Normalized)
0	0
2	0.6
4	45.7
8	100.0
12	72.9
16	58.6
20	36.6

Notes:

Operant conditioning with a food reward. Animals trained to peck a key during periods when click pairs were presented once per sec, with an inter-click-interval of 8 msec. This generalization gradient is for one male bullfinch given 15 generalization tests in extinction, each containing 140 stimulus presentations, 20 on each of seven stimulus values (inter-click-intervals). The 0 interval condition is equivalent to the presentation of a single click. The authors concluded from these data that the threshold for discrimination between a single click and a double click is between 2 and 4 msec.

Birds were also tested in discrimination between single and double clicks using both the method of constant stimuli and the method of limits. The threshold is given as the inter-click-interval of a double click which is just discriminable from a single click. The results are presented below.

Species	Procedure	N	Threshold (msec)
<i>Pyrrhula pyrrhula</i>	Limits	1	4.5
<i>Pyrrhula pyrrhula</i> (bullfinch)	Constant Stimuli	3	3.0
<i>Carduelis chloris</i> (greenfinch)	Limits	2	<2 to 4
<i>Columba livia</i> (pigeon)	Limits	2	6.0

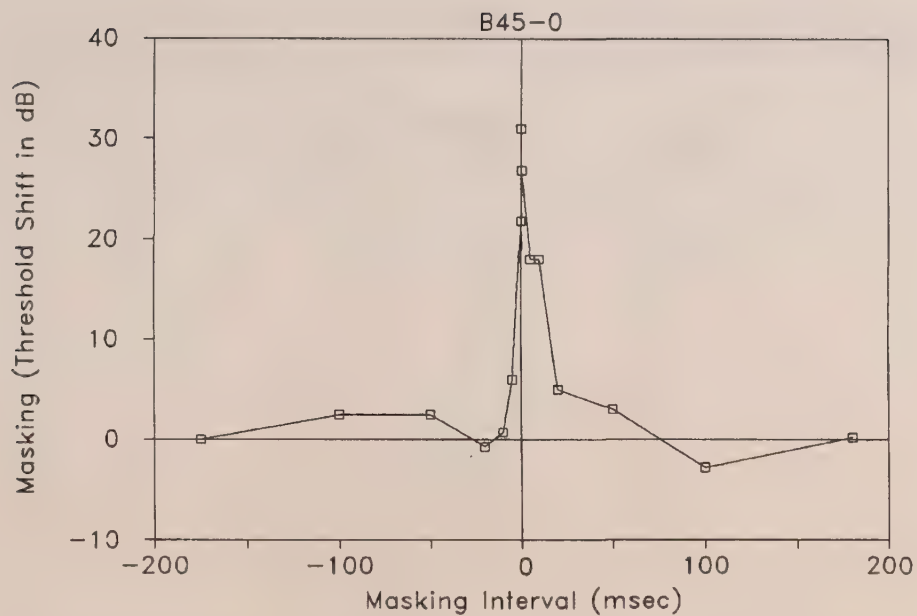


Fig. B45-0. Forward and backward masking in *Melopsittacus undulatus* (parakeet) (Dooling and Searcy, 1980).

Reference:

Dooling, R.J., and Searcy, M.H. (1980) Forward and backward auditory masking in the parakeet (*Melopsittacus undulatus*). *Hear. Res.* 3, 279-284.

Table B45-0. Forward and backward masking in *Melopsittacus undulatus* (parakeet) (Dooling and Searcy, 1980).

Masking Interval (msec)	Threshold Shift (dB)
-175	0
-100	2.5
-50	2.5
-20	-0.7
-10	0.7
-5	6
-0.2	21.8
0	31
0.2	26.8
5	18
10	18
20	5
50	3
100	-2.8
180	0.2

Notes:

Instrumental shock avoidance conditioning using the descending method of limits. Restrained animals were trained to bite a rod upon the presentation of a tone signal in order to avoid shock. Means: N=4.

Masker was noise bursts of 40 msec duration at 72 dB SPL. Signals were 5 msec tones. The time interval is the time between the end of the leading sound and the beginning of the following sound. The data are the differences between threshold for the probe signal in quiet and the masked threshold. The data points at ± 0.2 msec are for the conditions of zero time between the leading sound offset and the following sound onset. The data point at 0 (zero) is for a probe tone centered within the 40 msec masker.

Positive masking intervals (right of zero) indicate the case in which the masker preceded the signal (forward masking). Negative masking intervals indicate backward masking.

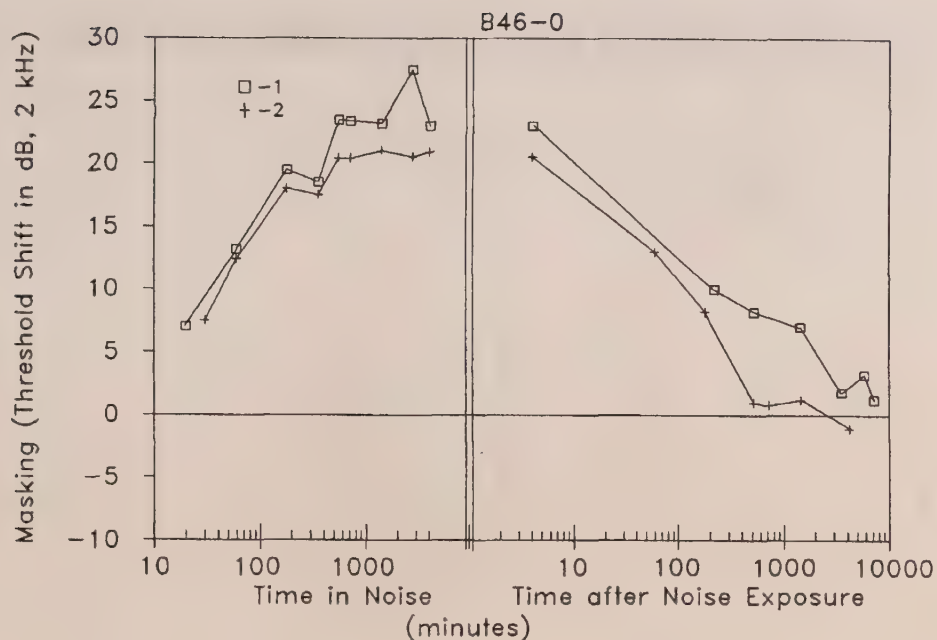


Fig. B46-0. Threshold shift as a function of the duration of noise exposure and as a function of the recovery time following noise exposure in *Melopsittacus undulatus* (parakeet) (Saunders and Dooling, 1974).

1- 96 dB noise exposure
2- 86 dB noise exposure

Reference:

Saunders, J., and Dooling, R.J. (1974) Noise-induced threshold shift in the parakeet (*Melopsittacus undulatus*). Proc. Nat. Acad. Sci. USA 71, 1962-1965.

Table B46-0. Threshold shift as a function of the duration of noise exposure and as a function of the recovery time following noise exposure in *Melopsittacus undulatus* (parakeet) (Saunders and Dooling, 1974).

Noise Exposure Duration or Recovery Time (minutes)	Threshold Shift (dB)	
	1	2
20	7	
30		7.5
60	13.2	12.4
180	19.5	18
360	18.5	17.5
560	23.5	20.4
720	23.4	20.4
1440	23.2	21
2880	27.5	20.5
4200	23	20.9
10000 or 0		
4	23	20.5
60		13
180		8.2
220	10	
520	8.2	1
720		0.8
1440	7	1.2
3500	1.8	
4200		-1.1
5800	3.2	
7200	1.2	

Notes:

Instrumental shock avoidance conditioning using a modified descending method of limits. Restrained animals were trained to avoid shock during the presentation of a tone signal by biting a bar. Four 16-week old animals, surgically deafened in the left ear.

Signal was one four sec tone presentation at 2 kHz, with 50 msec rise/fall times. Noise was 1/3 octave band centered at 2 kHz presented in a reverberation chamber. Asymptotic threshold shifts were 24.7 dB for the 96 dB noise exposure, and 20.5 dB for the 86 dB noise.

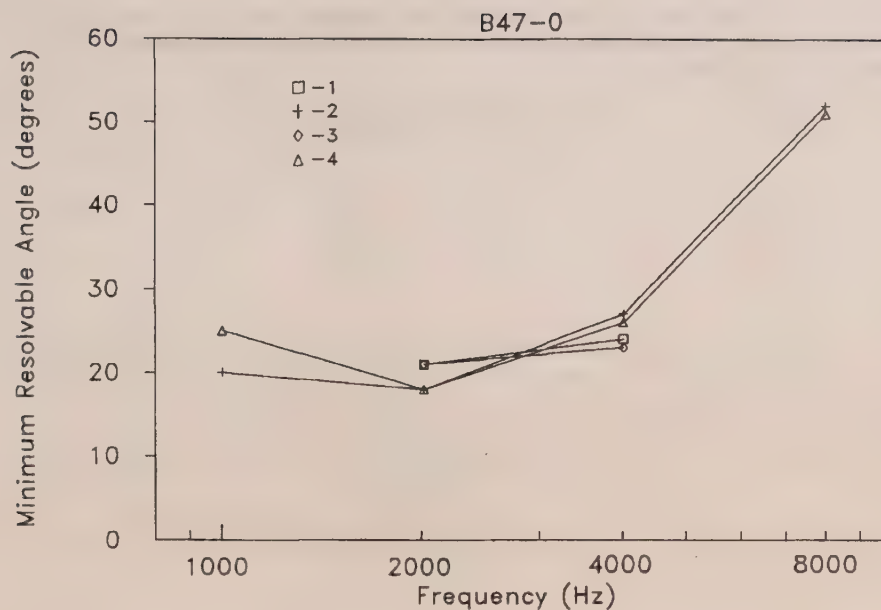


Fig. B47-0. The effect of tone duration on minimum resolution angle for azimuthal sound localization in *Parus major* (great tit) as a function of frequency (Klump, Windt, and Curio, 1986).

- 1- 40 msec duration
- 2- 100 msec
- 3- 150 msec
- 4- 300 msec

Reference:

Klump, G.M., Windt, W., and Curio, E. (1986) The great tit's (*Parus major*) auditory resolution in azimuth. *J. Comp. Physiol.* 158, 383-390.

Table B47-0. The effect of tone duration on minimum resolution angle for azimuthal sound localization in *Parus major* (great tit) as a function of frequency (Klump, Windt, and Curio, 1986).

Frequency (Hz)	Minimum Resolvable Angle (degrees)			
	1	2	3	4
1000		20		25
2000	21	18	21	18
4000	24	27	23	26
8000		52		51

Notes:

Operant conditioning with a food reward in a two alternative forced choice paradigm using the method of constant stimuli. Birds were trained to sit on a "waiting perch" (observing response) and to fly to one of two speakers placed symmetrically to the right and left of a midline. Thresholds were defined statistically ($p < 0.03$, two-tailed, binomial test) at each speaker separation. Testing took place in a chamber lined with sound absorbing wedges. Stimuli were 50 dB SPL tones with rise/fall times of 5 msec.

Localization ability was also investigated for four recorded calls ("seet", "scolding call," "mobbing call," and a "song element." Minimum resolvable angles were 45°, 16°, 20°, and 18°, respectively.

Means: N=2.

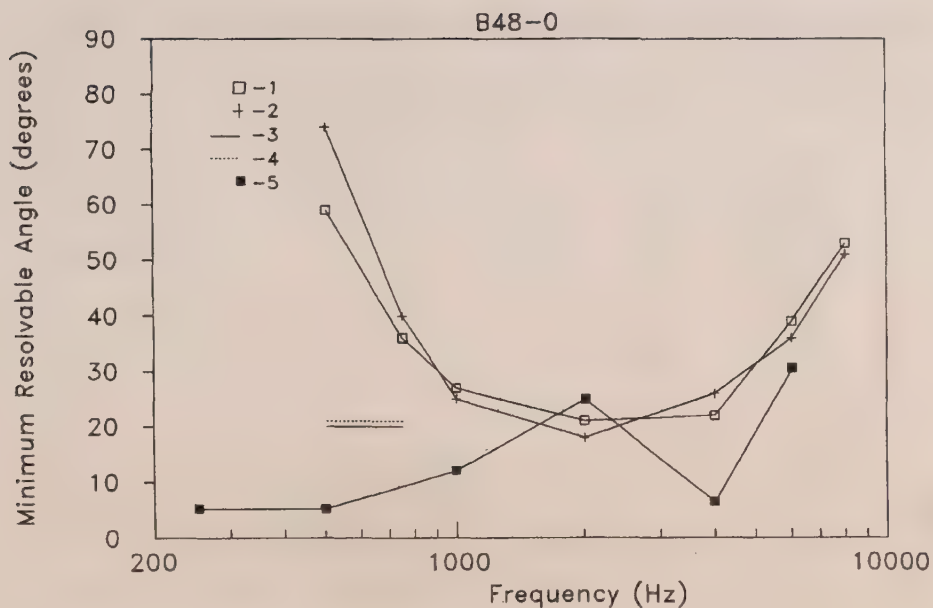


Fig. B48-0. The effect of tone frequency on the minimum resolvable angle for two bird species.

1-4- *Parus major* - great tit (Klump, Windt, and Curio, 1986)

1- Subject 1

2- Subject 2

3- Threshold for white noise, subject 1

4- Threshold for white noise, subject 2

5- *Columba livia* - homing pigeon (Lewald, 1987)

Reference:

Klump, G.M., Windt, W., and Curio, E. (1986) The great tit's (*Parus major*) auditory resolution in azimuth. *J. Comp. Physiol.* 158, 383-390.

Lewald, J. (1987) The acuity of sound localization in the pigeon (*Columba livia*). *Naturwissenschaften* 74, 296-297.

Table B48-0. The effect of tone frequency on the minimum resolvable angle for two bird species.

Frequency (Hz)	Minimum Resolvable Angle (degrees)				
	1	2	3	4	5
noise			20	21	
250					4.5
500	59	74			4.5
750	36	40			
1000	27	25			12.2
2000	21	18			25
4000	22	26			6.5
6000	39	36			30
8000	53	51			

Notes:

See Notes for Fig. B47-0.

1-4- Operant conditioning with a food reward in a two alternative forced choice paradigm using the method of constant stimuli. Birds were trained to sit on a "waiting perch" (observing response) and to fly to one of two speakers placed symmetrically to the right and left of a midline. Thresholds were defined statistically ($p < 0.03$, two-tailed, binomial test) at each speaker separation. Testing took place in a chamber lined with sound absorbing wedges. Stimuli were 300 msec, 50 dB SPL tones or white noise with rise/fall times of 5 msec.

5- Classically conditioned change in heart rate (to a shock UCS) using the descending method of limits. Signals were 3.5 sec pure tones with 10 msec rise/fall times at 70 dB SPL. Testing in a "sound-proof box." Medians: $N=5$. Greatest variability was found at 1 and 2 kHz (range: 5 to 45 degrees). Variability among subjects at the other frequencies was 5 to 15 degrees.

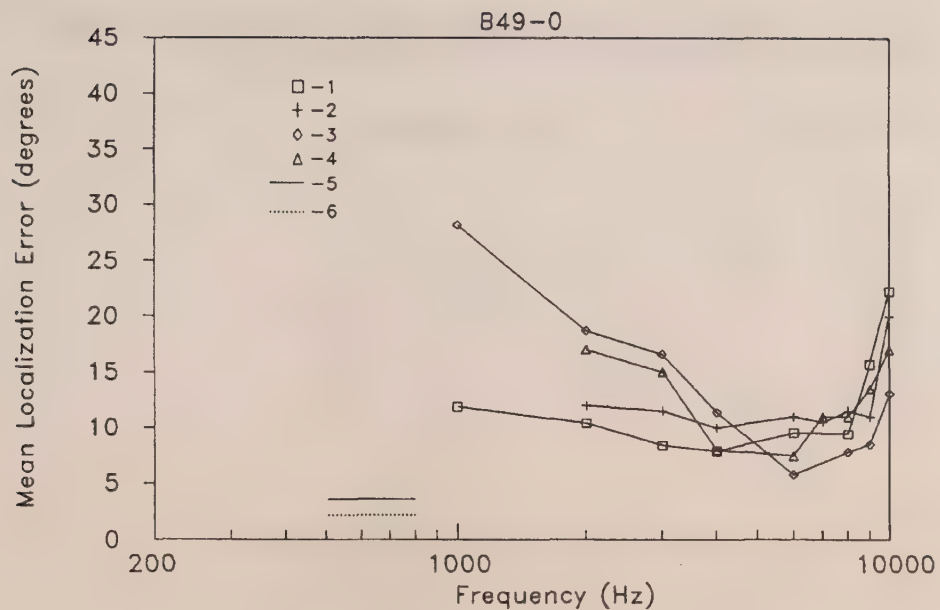


Fig. B49-0. Accuracy of sound localization in *Tyto alba* (barn owl) in azimuth and elevation for 75 msec and 1000 msec signals (Knudsen and Konishi, 1979).

- 1- Azimuth, 1000 msec tones
- 2- Azimuth, 75 msec tones
- 3- Elevation, 1000 msec tones
- 4- Elevation, 75 msec tones
- 5- Azimuth, 1000 msec noise
- 6- Elevation, 1000 msec noise

Reference:

Knudsen, E.I., and Konishi, M. (1979) Mechanisms of sound localization in the barn owl (*Tyto alba*). J. Comp. Physiol. 133, 13-21.

Table B49-0. Accuracy of sound localization in *Tyto alba* (barn owl) in azimuth and elevation for 75 msec and 1000 msec signals (Knudsen and Konishi, 1979).

Frequency (Hz)	Mean Error (degrees)					
	1	2	3	4	5	6
noise					3.6	2.2
1000	11.9		28.2			
2000	10.4	12	18.7	17		
3000	8.4	11.5	16.6	15		
4000	7.9	10	11.4	8		
6000	9.5	11	5.8	7.5		
7000		10.5		11		
8000	9.4	11.5	7.8	11		
9000	15.7	11	8.5	13.5		
10000	22.3	20	13.1	17		

Notes:

Head-turn toward sound source measured using "search coils," reinforced with food reward. Signals were tones or noise of the indicated duration, 2.5 msec rise/fall times, presented 20-40 dB above absolute threshold. Sources were randomly selected from eight locations displaced about 30° from 0° azimuth and 0° elevation. Data are mean head orientations in azimuth and elevation relative to source locations. Experiments conducted in a 5 x 3 x 3 meter IAC anechoic chamber.

Short duration signals (75 msec) defined "open loop" localization in which the signal had terminated by the time the animal had responded. Longer duration signals (1000 msec) defined "closed-loop" conditions in which the signal was still audible by the time the response had terminated.

For frequencies below 3000 and above 8000 Hz, each point is based on 9-18 successful trials. For all other frequencies, there were 24-45 trials.

N=1.

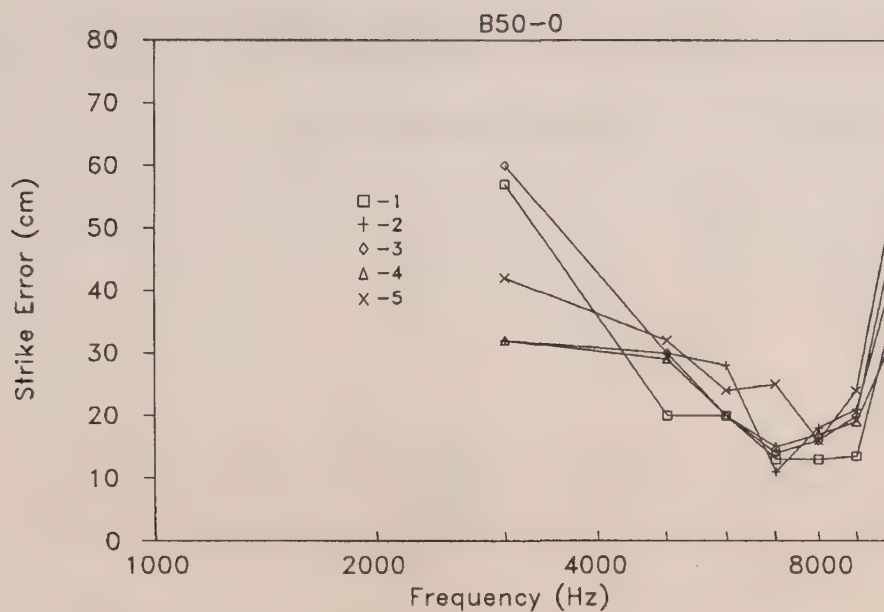


Fig. B50-0. The effects of frequency and source location on the ability of *Tyto alba* (barn owl) to locate sound sources (Konishi, 1973).

Speaker Azimuth Relative to Midline

- 1- 9° Left (continuous tone)
- 2- 5° Left (continuous tone)
- 3- 4° Right (continuous tone)
- 4- 10° Right (continuous tone)
- 5- 10° Right (tone burst)

Reference:

Konishi, M. (1973) Locatable and nonlocatable acoustic signals for barn owls. *Amer. Nat.* 107, 775-785.

Table B50-0. The effects of frequency and source location on the ability of *Tyto alba* (barn owl) to locate sound sources (Konishi, 1973).

Frequency (Hz)	Median Localization Error (cm)				
	1	2	3	4	5
3000	57	32	60	32	42
5000	20	30	30	29	32
6000	20	28	20	20	24
7000	13	11	14	15	25
8000	13	18	16	17	16
9000	13.5	21	20	19	24
10000	34	40	45	31	51

Notes:

Animals were trained to fly to loudspeakers from a 2 m high perch for a food reward. Experiments were conducted in a "soundproof and anechoic room," 5 m long, 3 m wide and 3 m high. Small speakers were located on the floor from 250 to 300 cm from the perch, at angles from 12° to the left to 17° to the right. Responses were recorded by noting which of 10 x 10 cm square areas on the floor the animal touched as it flew to the speaker broadcasting sound.

Signals were either 10 sec tones or repetitive tone bursts (50 or 80 msec bursts separated by 80 or 150 msec silent intervals) presented from 4 to 28 dB above detection threshold with 5 msec rise/fall times. The data show no particular advantage in locatability for the tone bursts relative to the 10 sec tones. Data points are median errors from 15 trials.

N=1.

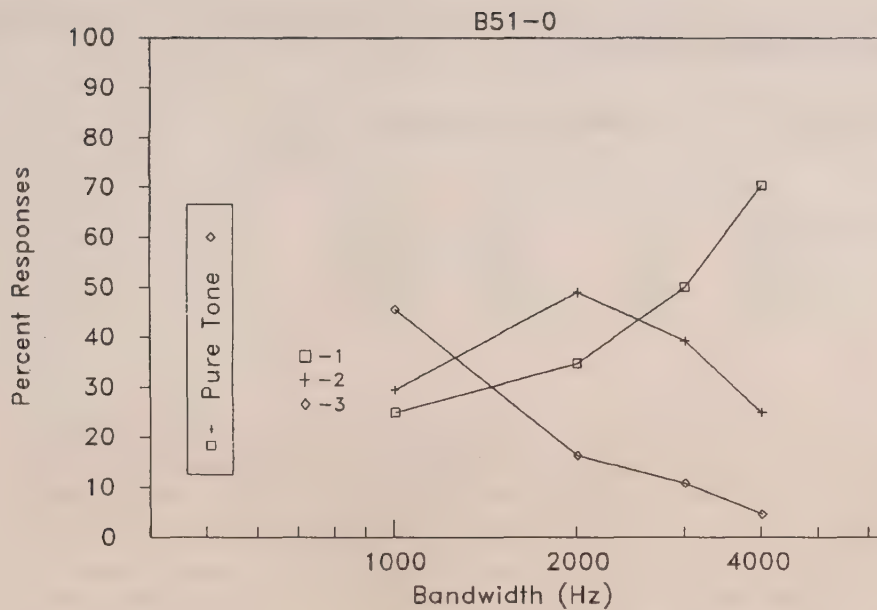


Fig. B51-0. The effects of signal bandwidth on the ability of *Tyto alba* (barn owl) to locate sound sources (Konishi, 1973).

- 1- Strikes within the area of 4, 10 x 10 cm squares surrounding the target
- 2- Strikes touching at least one of the 4 squares, plus some adjoining squares
- 3- Strikes falling entirely outside the 4 square zone surrounding the target

Reference:

Konishi, M. (1973) Locatable and nonlocatable acoustic signals for barn owls. *Amer. Nat.* 107, 775-785.

Table B51-0. The effects of signal bandwidth on the ability of *Tyto alba* (barn owl) to locate sound sources (Konishi, 1973).

Signal Bandwidth (Hz)	Percent Responses in Category		
	1	2	3
Pure Tone	18.3	21.7	60
1000	25	29.5	45.5
2000	34.8	48.9	16.3
3000	50	39.3	10.7
4000	70.3	25	4.7

Notes:

Animals were trained to fly to loudspeakers from a 2 m high perch for a food reward. Experiments were conducted in a "soundproof and anechoic room," 5 m long, 3 m wide and 3 m high. Small speakers were located on the floor from 250 to 300 cm from the perch, at angles from 12° to the left to 17° to the right. Responses were recorded by noting which of 10 x 10 cm square areas on the floor the animal touched as it flew to the speaker broadcasting sound.

Signals were either a 10 sec pure tone at 7000 Hz, or 10 sec noises centered at 7500 Hz with the indicated bandwidths. Tone presented at 4 dB SPL and noises presented at -12 dB SPL spectrum level, with 5 msec rise/fall times.

N=1.

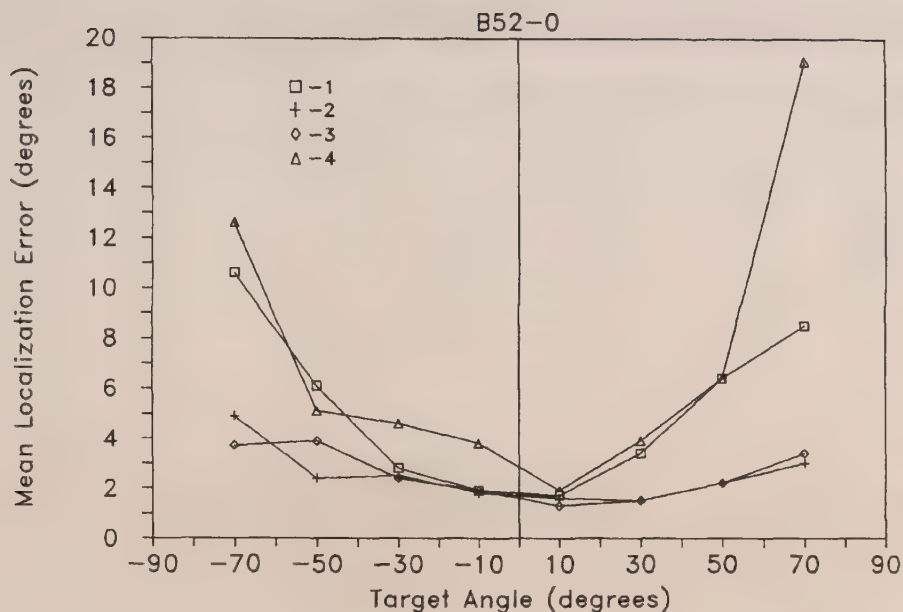


Fig. B52-0. The effect of sound source location on localization error in *Tyto alba* (barn owl) (Knudsen, Blasdel, and Konishi, 1979).

- 1- Horizontal plane location, azimuthal error
- 2- Horizontal plane location, elevation error
- 3- Vertical plane location, azimuthal error
- 4- Vertical plane location, elevation error

Reference:

Knudsen, E.I., Blasdel, G.G., and Konishi, M. (1979) Sound localization by the barn owl (*Tyto alba*) measured with the search coil technique. J. Comp. Physiol. 133, 1-11.

Table B52-0. The effect of sound source location on localization error in *Tyto alba* (barn owl) (Knudsen, Blasdel, and Konishi, 1979).

Source Angle (Degrees)	Mean Error (degrees)			
	1	2	3	4
-70	10.6	4.9	3.7	12.6
-50	6.1	2.4	3.9	5.1
-30	2.8	2.5	2.4	4.6
-10	1.9	1.8	1.9	3.8
10	1.7	1.6	1.3	1.9
30	3.4	1.5	1.5	3.9
50	6.4	2.2	2.2	6.4
70	8.5	3	3.4	19.1

Notes:

Head-turn toward sound source measured using "search coils," reinforced with food reward. Signals were noise bursts of 75 msec duration, 2.5 msec rise/fall times, presented 20-40 dB above absolute threshold. Data are mean head orientations in azimuth and elevation relative to source locations. Experiments conducted in a 5 x 3 x 3 meter IAC anechoic chamber.

Short duration signals (75 msec) defined "open loop" localization in which the signal had terminated by the time the animal had responded.

Each point based on from 21 to 27 responses.

N=1.

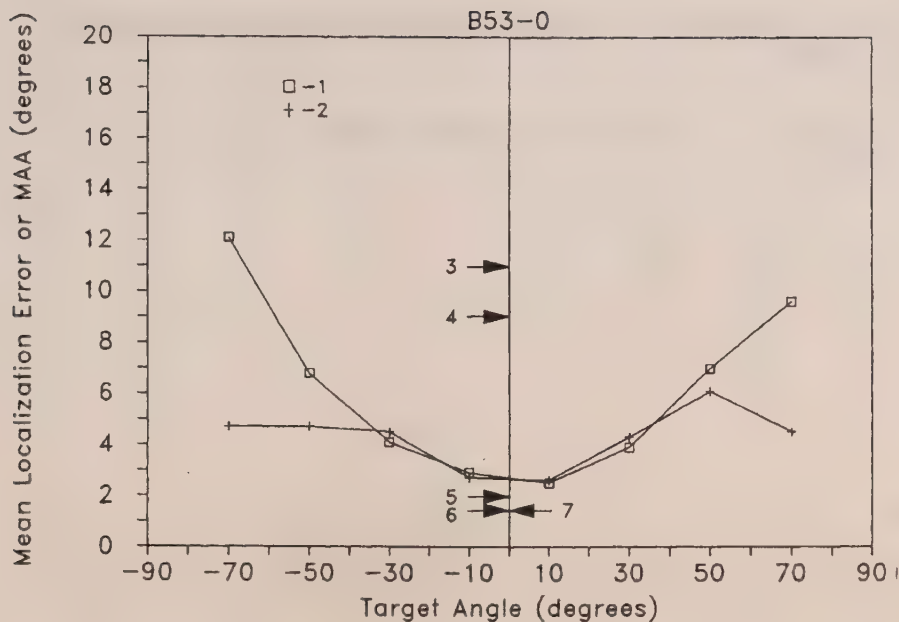


Fig. B53-0. Azimuthal sound source localization acuity for several nocturnal and diurnal raptors.

- 1- *Tyto alba* - barn owl, 75 msec noise
- 2- *Tyto alba* - barn owl, 1000 msec noise
(Knudsen, Blasdel, and Konishi, 1979)
- 3- *Falco sparverius* - American kestrel
- 4- *Buteo jamaicensis* - red-tailed hawk
- 5- *Circus cyaneus* - marsh hawk
- 6- *Tyto alba* - barn owl
- 7- *Asio flammeus* - short-eared owl
(Rice, 1982)

References:

- Knudsen, E.I., Blasdel, G.G., and Konishi, M. (1979) Sound localization by the barn owl (*Tyto alba*) measured with the search coil technique. *J. Comp. Physiol.* 133, 1-11.
- Rice, W.R. (1982) Acoustical location of prey by the marsh hawk: Adaptation to concealed prey. *The Auk* 99, 403-413.

Table B53-0. Azimuthal sound source localization acuity for several nocturnal and diurnal raptors.

Source Angle (degrees)	Mean Error or Minimum Audible Angle (degrees)						
	1	2	3	4	5	6	7
-70	12.1	4.7					
-50	6.8	4.7					
-30	4.1	4.5					
-10	2.9	2.7					
0			11	9	2	1.5	1.5
10	2.5	2.6					
30	3.9	4.3					
50	7	6.1					
70	9.6	4.5					

Notes:

1- Head-turn toward sound source measured using "search coils," reinforced with food reward. Signals were noise bursts of 75 msec duration, 2.5 msec rise/fall times, presented 20-40 dB above absolute threshold. These are "open-loop" conditions since the signal had terminated before the animal responded. Data are mean head orientation errors in azimuth relative to source locations in horizontal plane. Experiments conducted in a 5 x 3 x 3 meter IAC anechoic chamber.

2- Same as #1 above except that the 1000 msec signals defined a "closed-loop" condition in which the signal was still audible during the response. In both #1 and #2, each point is based on from 10 to 27 responses, and data are for one animal.

3-7- Operant response for a food reward using a method of constant stimuli. Animals were trained to fly from a perch to one of two floor-mounted loudspeakers broadcasting 200 msec bursts of broad band noise. In this forced-choice procedure with food reward for a correct response, there were 20 to 150 trials at each speaker separation for each animal. Data are means over two individuals of each species. Minimum audible angle defined as the smallest speaker separations giving 75% correct responses with 99% confidence.

This paper also reported that the two owl species and the marsh hawk tested were capable of some degree of vertical localization, while the kestrel and red-tailed hawk were not. Field experiments showed the marsh hawk capable of localizing without the aid of visual or olfactory cues. Note that the owls are nocturnal and the other species are diurnal raptors. The marsh hawk is unusual among diurnal raptors in its localization ability.

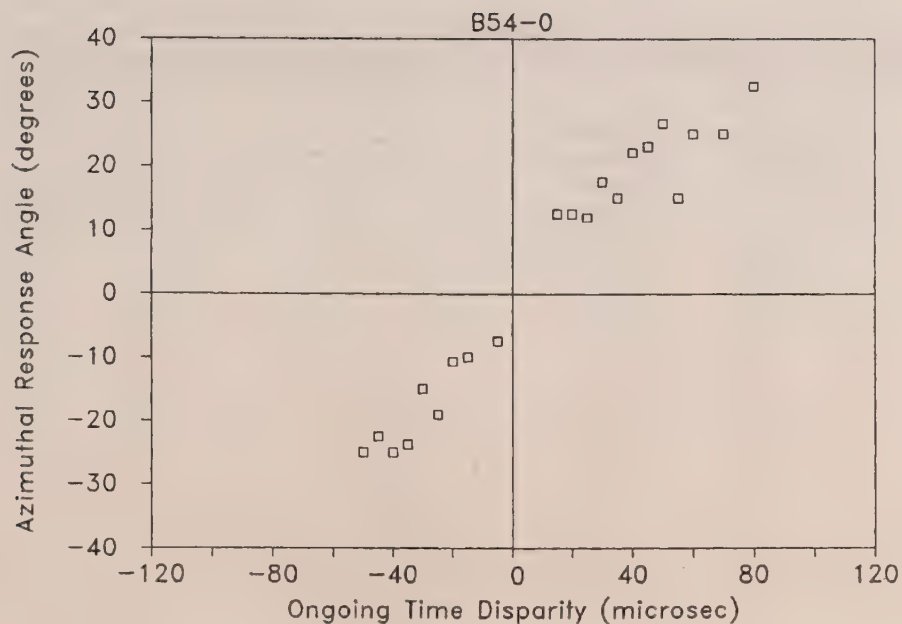


Fig. B54-0. Angle of saccadic head-turning caused by ongoing interaural time differences introduced through earphones in *Tyto alba* (barn owl) (Moiseff and Konishi, 1981).

Reference:

Moiseff, A., and Konishi, M. (1981) Neuronal and behavioral sensitivity to binaural time differences in the owl. *J. Neuroscience* 1, 40-48.

Table B54-0. Angle of saccadic head-turning caused by ongoing interaural time differences introduced through earphones in *Tyto alba* (barn owl) (Moiseff and Konishi, 1981).

Ongoing Time Disparity (microsec)	Mean Head Turn Angle (degrees)
-50	-25
-45	-22.5
-40	-25
-35	-23.75
-30	-15
-25	-19
-20	-10.7
-15	-10
-5	-7.5
15	12.5
20	12.5
25	12
30	17.5
35	15
40	22.1
45	23
50	26.7
55	15
60	25
70	25
80	32.5

Notes:

See Notes for Figs. B47-0 to B53-0.

In this experiment, animals were fitted with miniature earphones (Knowles BT-1759), and stimulated with noise (band-pass at 7000 Hz, 15 dB/octave roll-off). The noise envelope was identical at the two ears but the fine structure was interaurally delayed by the indicated times.

Data points are means extracted from a scatter plot presented in Moiseff and Konishi, 1981 (Fig. 10).

The best-fitting linear function is: Azimuth (degrees) = $(0.52 * \text{OTD}) - 1.48$ where OTD is the ongoing time difference in microsec. Based on 70 responses.

The head-turning response was measured by recording the projection of an infrared light-emitting diode mounted on the animal's head. The response was reinforced with food.

This experiment demonstrates that ongoing interaural time differences are sufficient for the owl to extract azimuthal information from a sound stimulus.

N=2.

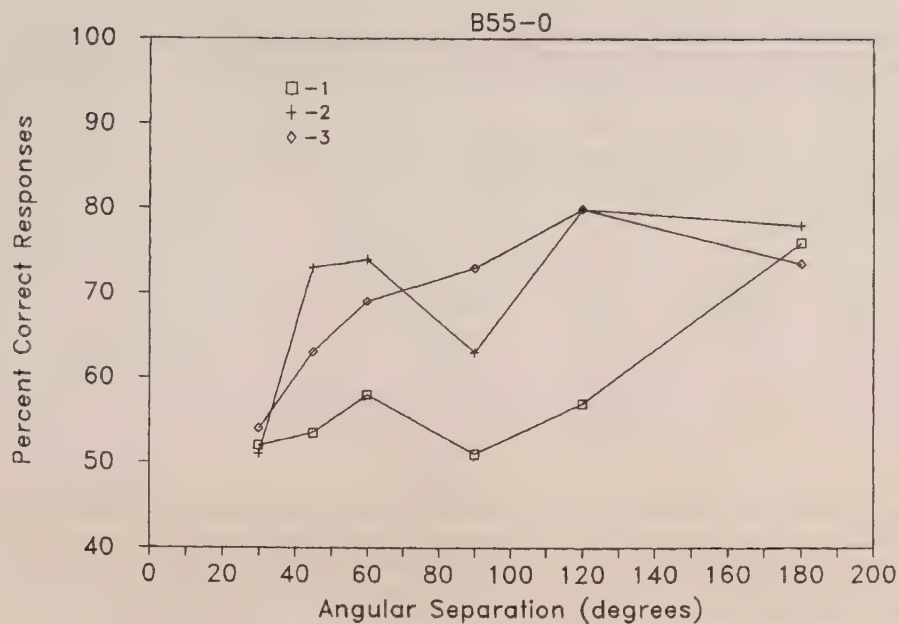


Fig. B55-0. Localization scores for *Colinus virginianus* (bobwhite quail) localizing tones and noise (Gatehouse and Shelton, 1978).

- 1- 1000 Hz tone
- 2- 2000 Hz tone
- 3- White noise

Reference:

Gatehouse, R.W. and Shelton, B.R. (1978) Sound localization in bobwhite quail (*Colinus virginianus*). Behav. Biol. 22, 533-540.

Table B55-0. Localization scores for *Colinus virginianus* (bobwhite quail) localizing tones and noise (Gatehouse and Shelton, 1978).

Angular Separation of Sources (degrees)	Percent Correct Responses		
	1	2	3
30	52	51	54
45	53.5	73	63
60	58	74	69
90	51	63	73
120	57	80	80
180	76	78	73.5

Notes:

Operant key-pecking for a food reward. Animals were trained to peck one of two keys corresponding in space to two loudspeakers to the left and right of the animal. A response on one key ipsilateral to the speaker broadcasting a 2 sec sound was rewarded. Training began with 180° speaker separation and continued until the animal discriminated sound source location at 70% correct or better. Then asymptotic performance was measured at each of several more narrow angular separations according to the method of constant stimuli.

Noise signal was 69 dB SPL, pulsed 10 per sec on a 50% duty cycle, with 5 msec rise/fall times. Tones were similarly shaped at 75 dB.

Means: N=2 males and N=4 females.

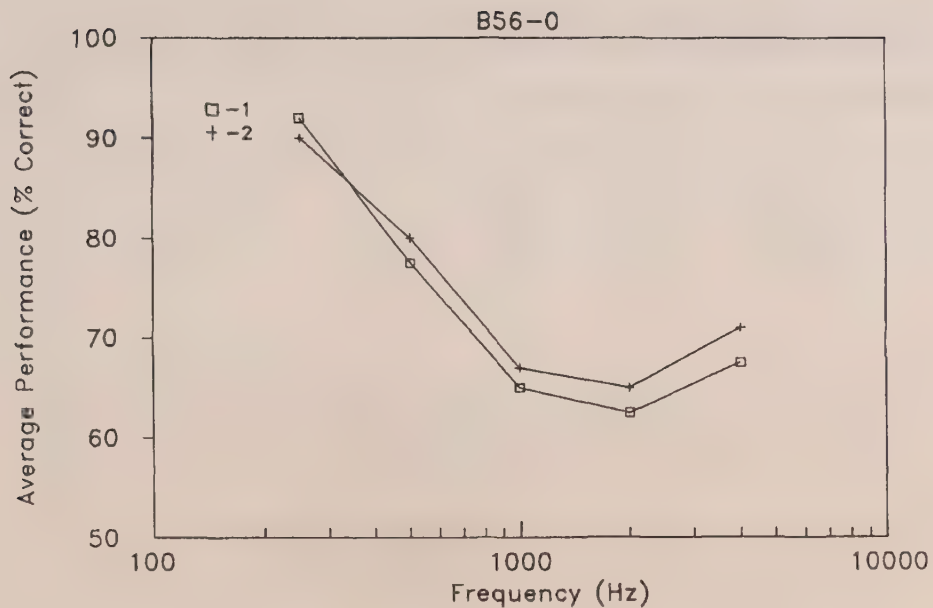


Fig. B56-0. Sound localization performance of *Columba livia* (pigeon) as a function of tone frequency (Jenkins and Masterton, 1979).

- 1- 40 dB above absolute detection level
- 2- 40 dB above threshold for significant localization behavior

Reference:

Jenkins, W.M., and Masterton, R.B. (1979) Sound Localization in pigeon (*Columba livia*).
J. Comp. Physiol. Psychol. 93, 403-413.

Table B56-0. Sound localization performance of *Columba livia* (pigeon) as a function of tone frequency (Jenkins and Masterton, 1979).

Frequency (Hz)	Average % Correct	
	1	2
250	92	90
500	77.5	80
1000	65	67
2000	62.5	65
4000	67.5	71

Notes:

Operant key pecking for a food reward. Animals were trained to peck an observing key which initiated sound from one of two loudspeakers separated by 120°. A subsequent response on the key ipsilateral to the activated loudspeaker was rewarded. The animals were required to approach the activated speaker to peck the correct key.

Signals 40 msec in duration, repeated twice per sec with rise/fall times of 25 msec.

1- This function plots percent correct responses as a function of tone frequency for signals presented 40 dB above the absolute detection thresholds.

2- This function determined at sound intensities 40 dB above the levels required for significant localization performance at each frequency.

These results suggest that signals of 1000 and 2000 Hz are particularly difficult to localize.

The authors noted that the animal's performance was best for low frequency tones, and poor for high frequency tones and noise. Discrimination was maintained even for very short duration signals, indicating that head movements during the sound presentation were not required for localization. The localization behavior was shown to be mediated by binaural hearing since plugging one ear abolished the discrimination. Since pigeons could be trained to localize both low (125 Hz) and high (8000 Hz) frequencies, the authors concluded that both interaural time and intensity cues, in isolation, could mediate sound localization in the pigeon.

Means: N=5.

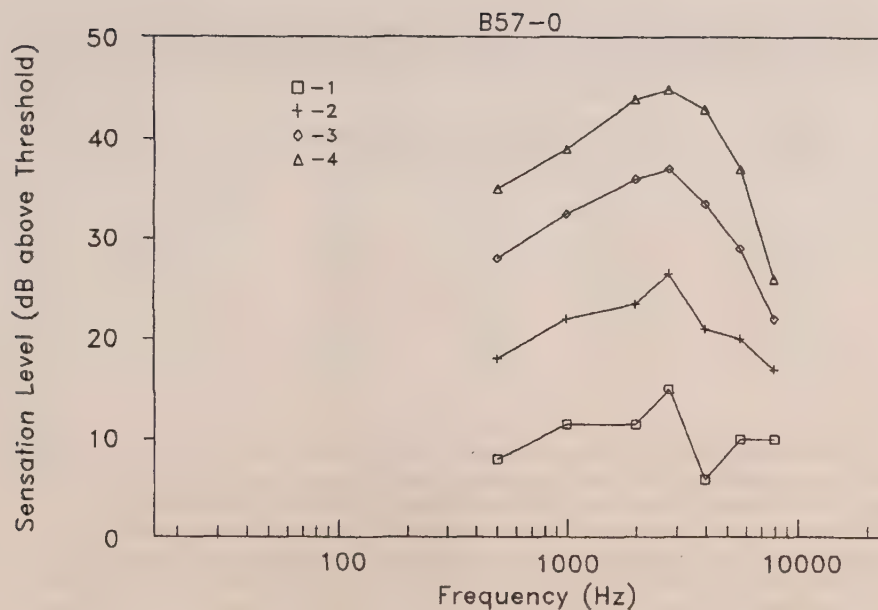


Fig. B57-0. Equal loudness contours in *Carpodacus mexicanus* (house finch) defined in terms of equal response latency (Dooling, Zoloth, and Baylis, 1978).

- 1- 2.5 msec latencies
- 2- 2.1 msec
- 3- 1.8 msec
- 4- 1.6 msec

Reference:

Dooling, R.J., Zoloth, S.R., and Baylis, J.R. (1978) Auditory sensitivity, equal loudness, temporal resolving power, and vocalizations in the house finch (*Carpodacus mexicanus*). J. Comp. Physiol. Psychol. 92, 867-876.

Table B57-0. Equal loudness contours in *Carpodacus mexicanus* (house finch) defined in terms of equal response latency (Dooling, Zoloth, and Baylis, 1978).

Frequency (Hz)	Sound Pressure (dB Sensation Level)			
	1	2	3	4
500	8	18	28	35
1000	11.5	22	32.5	39
2000	11.5	23.5	36	44
2800	15	26.5	37	45
4000	6	21	33.5	43
5700	10	20	29	37
8000	10	17	22	26

Notes:

Instrumental shock avoidance using a modified method of limits. Restrained animals were trained to avoid shock by biting a bar in the presence of pure tone stimuli. The response latency is a function of stimulus intensity, with higher intensities producing responses with shorter latencies. Response latency functions of stimulus intensity were obtained for each animal at each stimulus frequency, and the stimulus intensity required for four criterion response latencies determined. The data here are expressed as sound intensity above absolute threshold (sensation level). See Fig. B6-0. Means: N=4.

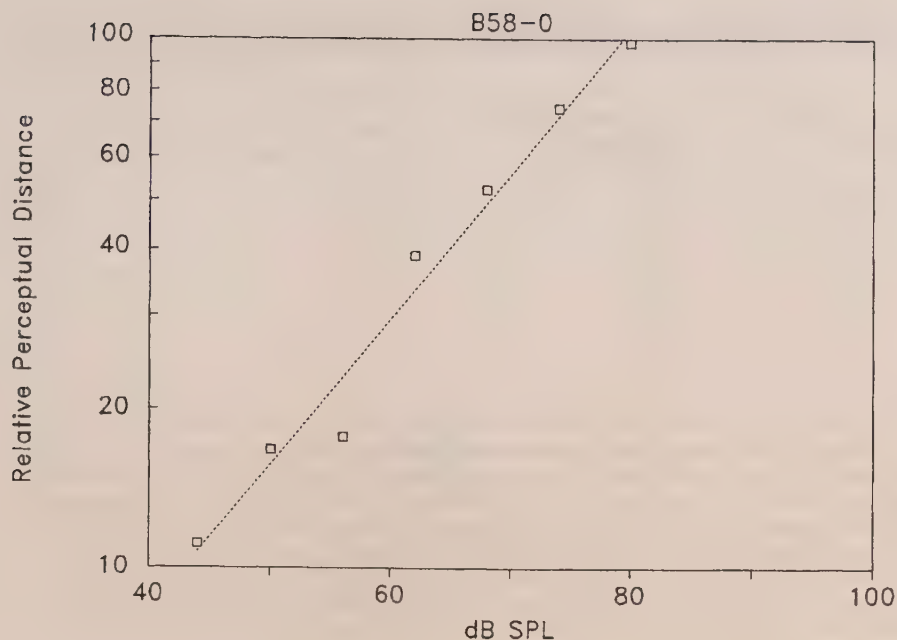


Fig. B58-0. Pure tone loudness function for *Melopsittacus undulatus* (parakeet) derived using multidimensional scaling (Dooling, Brown, Park, Okanoya, and Soli, 1987).

Reference:

Dooling, R.J., Brown, S.D., Park, T.J., Okanoya, K., and Soli, S. (1987) Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): I. Pure tones. *J. Comp. Psychol.* 101, 1-11.

Table B58-0. Pure tone loudness function for *Melopsittacus undulatus* (parakeet) derived using multidimensional scaling (Dooling, Brown, Park, Okanoya, and Soli, 1987).

Sound Pressure (dB SPL)	Relative Perceptual Distance (%)
44	11.1
50	16.7
56	17.7
62	39
68	52
74	74
80	100

Notes:

Operant key-pecking for a food reward. Animals were presented with a pair of brief stimuli which were either the same or different in level. If they were different, the animal was trained to peck a key within 2 sec. If they were the same, a response within 2 sec was punished with a time-out. After training with two stimuli of different intensity (80 dB and 68 dB), animals were then tested on a set of eight stimuli differing only in intensity (35 dB to 80 dB in 6 dB steps). All combinations of the eight stimuli defined a matrix, and 6 matrices were averaged for each subject. The latency to respond "different" was measured, and transformed logarithmically. These data were subjected to a multidimensional scaling program ("SINDSCAL"), and "perceptual distances" among the stimulus set computed. These distances were normalized as percentages.

The linear function best-fitting the data is: $L = kP^{0.28}$, where L is perceptual distance, and P is sound intensity.

Stimuli were 200 msec 2000 Hz pure tones with rise/fall times of 5 msec.

Means: N=2.

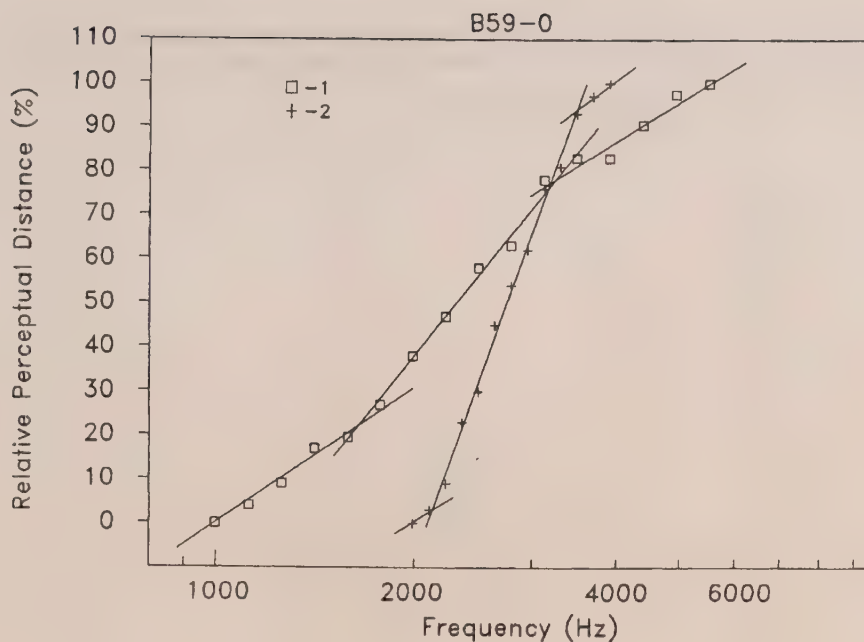


Fig. B59-0. Pure tone pitch scales for *Melopsittacus undulatus* (parakeet) derived using multidimensional scaling (Dooling, Brown, Park, Okanoya, and Soli, 1987).

- 1- Pitch scale for a set of 16 stimuli from 1000 to 5660 Hz
- 2- Pitch scale for a set of 13 stimuli from 2000 to 4000 Hz

Reference:

Dooling, R.J., Brown, S.D., Park, T.J., Okanoya, K., and Soli, S. (1987) Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): I. Pure tones. *J. Comp. Psychol.* 101, 1-11.

Table B59-0. Pure tone pitch scales for *Melopsittacus undulatus* (parakeet) derived using multidimensional scaling (Dooling, Brown, Park, Okanoya, and Soli, 1987).

Frequency (Hz)	Relative Perceptual Distance (%)	
	1	2
1000	0	
1122	4	
1260	9	
1414	17	
1590	19.5	
1782	27	
2000	38	0
2119		3
2245	47	9
2378		23
2520	58	30
2670		45
2828	63	54
2997		62
3175	78	76
3364		81
3564	83	93
3775		97
4000	83	100
4490	90.5	
5040	97.5	
5660	100	

Notes:

Operant key-pecking for a food reward. Animals were presented with a pair of brief stimuli which were either the same or different in frequency. If they were different, the animal was trained to peck a key within 2 sec. If they were the same, a response within 2 sec was punished with a time-out. Animals were tested on a set of 16 (#1) or 13 (#2) stimuli differing only in frequency (1000 to 5700 Hz in 1/6 octave steps, or 2000 to 4000 Hz in 1/12 octave steps). All combinations of the stimuli defined a matrix, and 5 matrices were averaged for each subject. The latency to respond "different" was measured, and transformed logarithmically. These data were subjected to a multidimensional scaling program ("SINDSCAL"), and "perceptual distances" among the stimulus set computed. These distances were normalized as percentages.

Each function was best-fit (by the authors) with three linear functions for each set of data. The authors note that the slope change in each case occurs at about the same frequency locations.

Stimuli were 200 msec pure tones at 76 dB SPL with rise/fall times of 5 msec.

Means: N=3.

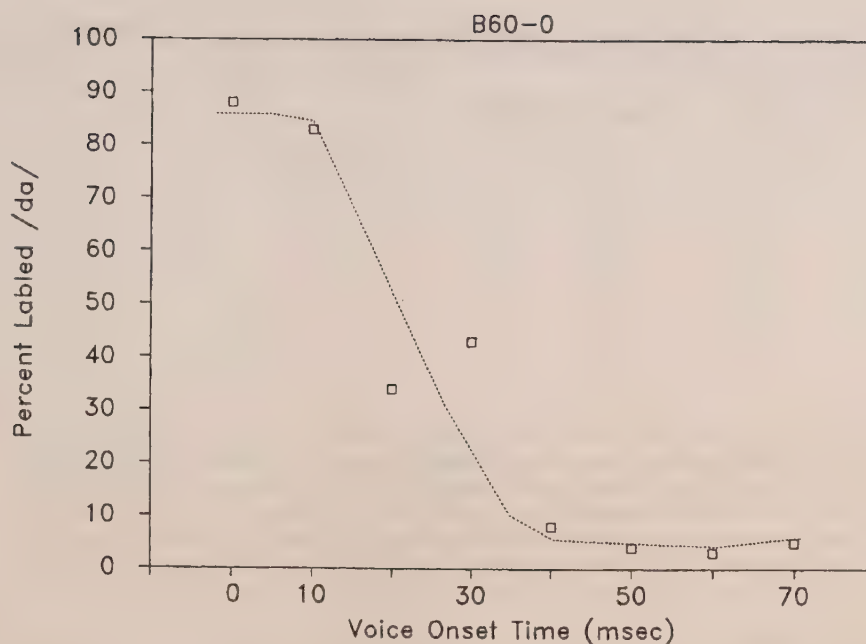


Fig. B60-0. The effect of voice onset time on the "labeling" of phonemes /da - ta/ by *Melopsittacus undulatus* (parakeet) (Dooling, 1986).

Reference:

Dooling, R.J. (1986) Perception of vocal signals by budgerigars (*Melopsittacus undulatus*). J. Exp. Biol. 45, 195-218.

Table B60-0. The effect of voice onset time on the "labeling" of phonemes /da - ta/ by *Melopsittacus undulatus* (parakeet) (Dooling, 1986).

Voice Onset Time (msec)	Percent Labeled /da/
0	88
10	83
20	34
30	43
40	8
50	4
60	3
70	5

Notes:

Operant conditioning with a food reward. Animals were trained to begin a trial by pecking an "observing" key. They were trained to respond on another key within 4 sec if the stimulus was a synthesized speech token with 0 msec voice onset time (VOT). This sounds to a human listener like the sound /da/. Simultaneously they were trained to withhold response for a similar speech token with a 70 msec VOT (sounds like /ta/). In blocks of 50 trials, 6 of these (at random) were VOTs intermediate between 0 and 70 msec. The percentage of responses to these as if they were 0 msec VOT are listed and plotted above.

The author notes that the VOT corresponding to a transition between /da/ and /ta/ is shorter in parakeet than in humans, chinchillas (Kuhl and Miller, 1975), or macaques (Kuhl and Padden, 1982).

Means: N=2.

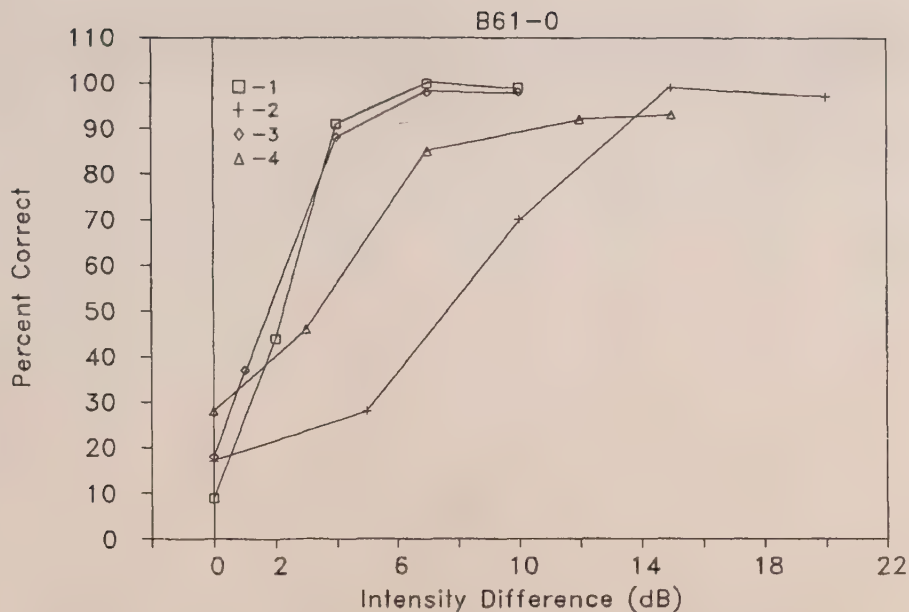


Fig. B61-0. Psychometric functions for intensity discrimination of increments and decrements in *Agelaius phoeniceus* (redwing blackbird), and *Columba livia* (pigeon) (Hienz, Sinnott, and Sachs, 1980).

- 1- *Agelaius phoeniceus* - redwing blackbird, intensity increments
- 2- *Agelaius phoeniceus* - redwing blackbird, intensity decrements
- 3- *Columba livia* - pigeon, intensity increments
- 4- *Columba livia* - pigeon, intensity decrements

Reference:

Hienz, R.D., Sinnott, J.M., and Sachs, M.B. (1980) Auditory intensity discrimination in blackbirds and pigeons. *J. Comp. Physiol. Psychol.* 94, 993-1002.

Table B61-0. Psychometric functions for intensity discrimination of increments and decrements in *Agelaius phoeniceus* (redwing blackbird), and *Columba livia* (pigeon) (Hienz, Sinnott, and Sachs, 1980).

Intensity Difference (dB)	Percent Correct			
	1	2	3	4
0	9	17	18	28
1			37	
2	44			
3				46
4	91		88	
5		28		
7	100		98	85
8				
10	99	70	98	
12				92
15		99		93
20		97		

Notes:

Operant conditioning for a food reward using the method of constant stimuli. Functions are for an individual redwing (#1 and #2) at 2 kHz, and for an individual white Carneaux pigeon (#3 and #4) at 1 kHz.

The background stimuli were tones, 250 msec in duration with 20 msec rise/fall times, separated by 250 msec of silence. Signals consisted of the pulsed tones alternating in intensity between the standard background intensity and an incremented or decremented intensity. Intensity decrements were difficult for the animals to detect, and failed to maintain conditioned responses in some subjects. Note that the slopes of the psychometric functions are lower for decrement detection than for increment detection. Note also that the percent correct values at 0 dB intensity difference (an estimate of the false alarm rate) are higher for decrement than for increment detection.

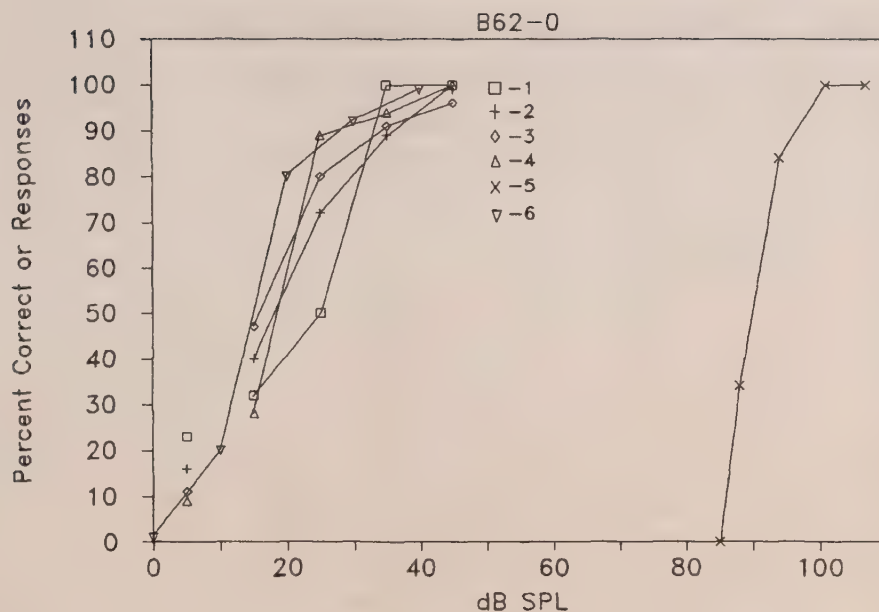


Fig. B62-0. Psychometric functions for tone detection in quiet for two bird species.

- 1-4- *Agelaius phoeniceus* - redwing blackbird, 1 kHz (Hienz, Sinnott, and Sachs, 1977)
 Four replications, ordered.
 5- *Columba livia* - pigeon, 1 Hz (infrasound) (Kreithen and Quine, 1979)
 6- *Cyanocitta cristata* - blue jay, 1 kHz (Cohen, Stebbins, and Moody, 1978)

References:

- Cohen, S.M., Stebbins, W.C., and Moody, D.B. (1978) Audibility thresholds for the blue jay. *The Auk* 95, 563-568.
 Hienz, R.D., Sinnott, J.M., and Sachs, M.B. (1977) Auditory sensitivity of the red-winged blackbird (*Agelaius phoeniceus*), and brown-headed cowbird (*Molothrus ater*). *J. Comp. Physiol. Psychol.* 91, 1365-1376.
 Kreithen, M.L., and Quine, D.B. (1979) Infrasound detection by the homing pigeon: A behavioral audiogram. *J. Comp. Physiol.* 129, 1-4.

Table B62-0. Psychometric functions for tone detection in quiet for two bird species.

Sound Pressure (dB SPL)	Percent Correct or Percent Responses					
	1	2	3	4	5	6
0						1
5	23	16	11	9		
10						20
15	32	40	47	28		
20						80
25	50	72	80	89		
30						92
35	100	89	91	94		
40						99
45	100	99	96	100		
85					0	
88					34	
94					84	
101					100	
107					100	

Notes:

1-4- Operant conditioning for a food reward using the method of constant stimuli. Go-left, go-right procedure. In this procedure, three pecking keys were used, a right, center, and left key. A trial began with illumination of the center key. Pecking the center key (observing response) caused a tone to be presented with a probability of 0.5. A peck on the right key in the presence of the tone was a "hit," while left key peck a "miss." When no tone was presented ("catch trial"), a peck on the right key was a "false alarm" and a peck on the left key was a "correct rejection." Data are for one male. #1-#4 show the data from sessions 5, 6, 7, and 8, respectively. The unconnected points show the false alarm rates averaged over a session in which four different signal intensities were presented.

5- Two loudspeakers operated into a sealed chamber containing the bird. These operated in phase (both raising and then lowering the pressure in the box) to produce sound pressure fluctuations as low as 0.05 Hz. When these were operated in a push-pull manner (one raising the pressure and the other lowering the pressure in the box), no net pressure change occurred. This served as a control condition for spurious speaker noises.

Classical cardiac conditioning (bradycardia) with shock as the UCS using a type of adaptive tracking psychophysics. For this individual pigeon, a positive response was defined as a heart rate 12 beats-per-min above the highest instantaneous rate for the 10 sec period preceding the signal presentation.

6- Operant conditioning for a food reward using the method of constant stimuli. An animal was trained to initiate a trial by grasping a metal bar with its beak and twisting it. A tone signal was turned on between 0.5 and 2.5 sec later, and a correct response was defined as releasing the bar during the 0.3 sec, 1kHz stimulus tone presentation.

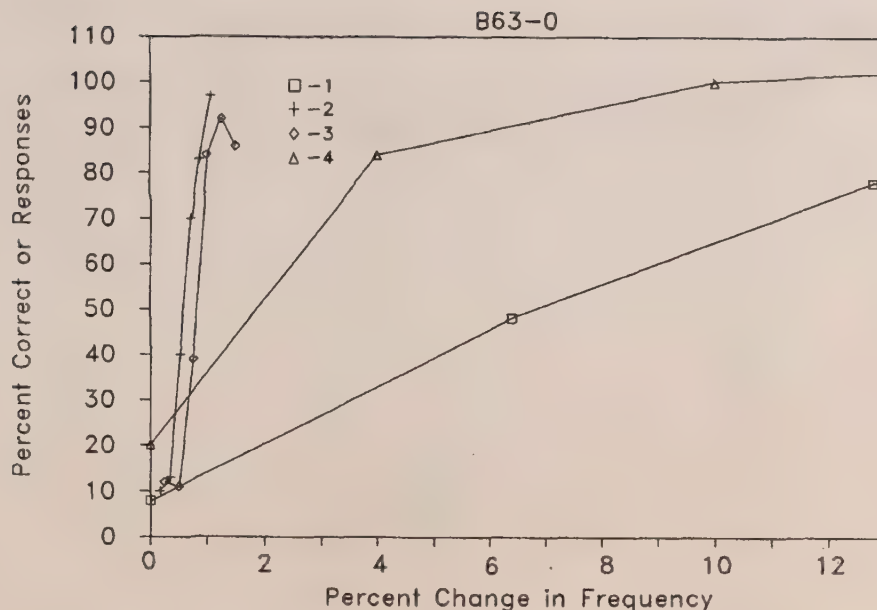


Fig. B63-0. Psychometric functions in frequency discrimination for several bird species.

- 1- *Agelaius phoeniceus* - redwing blackbird, 250 Hz (Sinnott, Sachs, and Hienz, 1980)
- 2- *Melopsittacus undulatus* - parakeet, 2.86 kHz (Dooling and Saunders, 1975)
- 3- Same as #2, 4 kHz
- 4- *Columba livia* - pigeon, 10 Hz (Quine and Kreithen, 1981)

References:

- Dooling, R.J., and Saunders, J.C. (1975) Hearing in the parakeet (*Melopsittacus undulatus*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations. *J. Comp. Physiol. Psychol.* 88, 1-20.
- Quine, D.B., and Kreithen, M.L. (1981) Frequency shift discrimination: Can homing pigeons locate infrasounds by doppler shifts? *J. Comp. Physiol.* 141, 153-155.
- Sinnott, J.M., Sachs, M.B., and Hienz, R.D. (1980) Aspects of frequency discrimination in passerine birds and pigeons. *J. Comp. Physiol. Psychol.* 94, 401-415.

Table B63-0. Psychometric functions in frequency discrimination for several bird species.

Frequency Change (%)	Percent Correct or Percent Responses			
	1	2	3	4
0	8			20
0.175		10		
0.25			12	
0.35		13		
0.5			11	
0.52		40		
0.7		70		
0.75			39	
0.87		83		
1			84	
1.05		97		
1.25			92	
1.5			86	
4				84
6.4	48			
10				100
12.8	78			
25.6	98			
32				100
46	95			

Notes:

Percent changes in frequency above 13 are not plotted but appear in the table.

1- Operant conditioning for a food reward using the method of constant stimuli (go, no-go). N=1.

A constant background stimulus consisting of tone bursts (250 msec on, 250 msec off, 20 msec rise/fall times) at the "standard" frequency of 250 Hz was presented. The signal consisted of a period during which the frequency of the bursts alternated between the standard and a comparison (higher) frequency. 50 dB sensation level.

2- Instrumental shock avoidance conditioning using the method of limits psychophysical procedure. A restrained bird was trained to bite a rod upon the presentation of a tone in order to avoid shock.

A background stimulus (tone bursts (100 msec on, 400 msec off, 20 msec rise/fall times) at the "standard" frequency of 2.86 kHz was presented. The signal was an alternation between the standard and comparison (upward shift) frequency at 60 dB sensation level.

3- Same as #2, 4 kHz.

4- Infrasound frequency discrimination. Classical cardiac conditioning (bradycardia) with a shock UCS using the method of constant stimuli. See Notes for Fig. B5-0 and B62-0 for more details on the method. Background consisted of a continuous pure tone at 30 dB sensation level. Signal was smoothly shifted upward in frequency within 800 msec.

Hearing in Mammals

The hearing abilities of mammals have been studied more intensely than the abilities of other vertebrates. This attention reflects the facts that many of the experimental methods for behavior control and analysis were first developed for mammals, and mammals have been the primary animal models for human hearing and hearing impairment. The hearing and sound discrimination capacities of mammals also provide important data for an analysis of the neural correlates and causes of auditory perception. The psychoacoustics of non-human mammals provides an important logical connection between auditory neurophysiology (most often carried out on non-human animals) and human psychoacoustics. Presently, neurophysiological data from cats, monkeys and various other mammals are often used to test hypotheses about the neural codes and mechanisms underlying human hearing abilities. With sufficient animal psychophysical data, however, it becomes possible to directly evaluate neural models for auditory perception using neurophysiological and psychophysical data from the same species (e.g. the cat). These relations can then help form stronger hypotheses on the neural mechanisms of hearing in the human. Theories which ignore the data from animal psychophysics and proceed directly from animal physiology to human hearing will have to remain tentative and of limited value.

Questions of the general validity of animal psychophysics seem most acute with regard to hearing in mammals since we tend to look to the mammals for hearing functions most like our own. There are several major dimensions of concern in assessing the validity of animal psychophysical thresholds. First, there is a great concern that the methodologies used in animal psychophysics be comparable if not identical with those used to assess human hearing. There now can be no doubt that many of the psychophysical paradigms routinely used to study detection and discrimination in human subjects can be used with animal subjects. For example, two-alternative forced choice tasks in which independent estimates of sensitivity and response bias can be obtained have often been applied in studies of animal hearing. In these cases, at least, further questions on the validity of the thresholds obtained would seem to fall into two categories; one concerning the motivation of the subjects, and one concerning the general cognitive capabilities of the subjects.

It is often assumed that appetitive, operant conditioning (for food or water reward) provides the best method for properly motivating animal subjects so that their behavior can be strictly controlled by stimulus variables. Although this assumption makes some intuitive sense, it has yet to be tested rigorously. Throughout this book, there are examples of thresholds determined in the same lab using different conditioning paradigms. There has yet to be a clear demonstration that one or the other type of conditioning or training results in consistently more valid (usually lower) thresholds. For example, of the 10 audiograms published for the cat, five were determined using operant conditioning for food, and five were determined using shock avoidance (Figs. M11-0 and M12-0). The mean best threshold for the operant method is -15.9 dB SPL and the mean for the avoidance method is -14.6, with an overall standard deviation of about 7 dB. Although this hardly represents an experiment on this point, the results do

not encourage the view that clear differences will be found if looked for carefully.

Thresholds such as these for the cat, which are equal to or below those measured for human subjects, help to establish the validity of animal psychophysics, at least for measures of absolute threshold. If it is believed that conditioning paradigms used with animals somehow underestimate "true" threshold sensitivity, then one would have to believe that the lowest absolute thresholds for the cat were significantly below -15 dB SPL. Such extreme sensitivity would be difficult to accept.

While accepting the validity of absolute threshold measures for non-human animals, a critic could go on to argue that the sensitivity of animals on more complex discrimination tasks requiring more memory or other cognitive skills could still be underestimated by the conditioning methods typically used. Such a critic could argue, for example, that the rather high frequency discrimination thresholds for cat and monkey compared with the human (M65-0 and M66-0) reflect differences in cognitive performance rather than in sensory capacity. This is an important issue in the choice of the psychophysical results that are used as criteria for models of auditory information processing. If the human thresholds are better estimates of frequency resolution in the cat than the cat thresholds themselves are, then one is justified in using the human thresholds as criteria for models based on cat neurophysiology. However, if the cat thresholds are valid measures of sensory capacity, then it would be logical to use them in as criteria in the neurophysiological models. Although these and related questions cannot yet be answered with certainty, it is noteworthy that the frequency discrimination thresholds of the porpoise (M68-0) and the elephant (M65-0) equal or fall below those of the human at some frequencies (C3-0). This indicates: 1) that the common conditioning methods applied to non-human animals are capable of revealing human-like sensitivity, 2) that there likely are real species differences among non-humans that span a considerable range, and 3) that the human is not uniquely sensitive among mammals in frequency discrimination. These comparisons illustrate one way in which animal psychophysical studies on a wide range of species and tasks can be valuable in advancing our understanding of hearing mechanisms. It is hoped that the reader will find many other comparative data in the pages of this review that will lead to an increased understanding of vertebrate hearing in general, and thus of human hearing.

The structures and functions of the ears of mammals will be familiar to most readers, so I will forego a brief description of the type introducing the previous sections. It will be enough to point out that the mammals are the most diverse class with regard to upper and lower frequency limit of hearing, bandwidth, and the frequency range of best sensitivity (C1-0). In many cases, mammals also differ widely in cochlear length, number of hair cells, number of ganglion cells, and in innervation density throughout the cochlea. In addition, mammals populate quite different habitats (with their characteristic acoustic properties), make their living at different times of day and night, and differ greatly in head size, outer ear structure, and in the relative sizes of auditory brain nuclei. These and other factors may contribute to many of the species differences in detection and discrimination capacities that are illustrated in the following pages.

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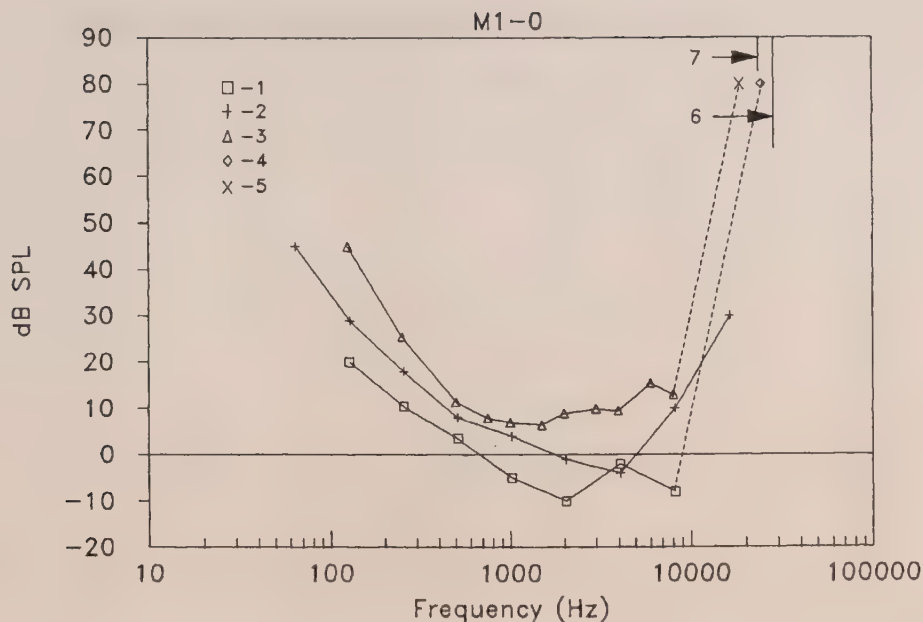


Fig. M1-0. Audiograms for *Pan troglodytes* (chimpanzee) and the human.

- 1- *Pan troglodytes* - Chimpanzee (Elder, 1934)
- 2- *Homo sapiens* - human, Minimum Audible Field (Sivian and White, 1933)
- 3- *Homo sapiens* - human, headphones (ANSI 3.6, 1969)
- 4- *Pan troglodytes* - chimpanzee (Farrer and Prim, 1965)
- 5- *Homo sapiens* - human, headphones (Farrer and Prim, 1965)
- 6- *Pan troglodytes* - chimpanzee (Elder, 1935)
- 7- *Homo sapiens* - human (Elder, 1935)

References:

- American National Standards Institute (ANSI), Audiometer Standard 3.6 (1969).
- Elder, J.H. (1934) Auditory acuity of the chimpanzee. *J. Comp. Physiol. Psychol.* 17, 157-183.
- Elder, J.H. (1935) The upper limit of hearing in chimpanzee. *Amer. J. Physiol.* 112, 109-115.
- Farrer, D.N., and Prim, M.M. (1965) A preliminary report on auditory frequency threshold comparisons of humans and pre-adolescent chimpanzees. Technical Report of the 6571st Aeromedical Research Lab., ARL-TR-65-6, 1-13.
- Sivian, L.J. and White, S.D. (1933) On minimum audible fields. *J. Acoust. Soc. Amer.* 4, 288-321.

Table M1-0. Audiograms for *Pan troglodytes* (chimpanzee) and the human.

Frequency (Hz)	dB SPL						
	1	2	3	4	5	6	7
64		45					
125			45				
128	20	29					
250			25.5				
256	10.5	18					
500			11.5				
512	3.5	8					
1000			7				
1024	-5	4					
1500			6.5				
2000			9				
2048	-10	-1					
3000			10				
4000			9.5				
4096	-2	-4					
6000			15.5				
8000			13				
8192	-8	10					
16384		30					
18780					80		
22900							U
24470				80			
28900						U	

Notes: (U = unspecified)

1- Operant conditioning for food using method of constant stimuli. Animals trained to press a key in the presence of a tone. Signals presented through headphone using a Western Electric 2-A audiometer. Means: N=3. There was no absolute calibration for human thresholds (data from the studies of Bunch (1931) and Drury (1925) were used as a reference). The data plotted were obtained by assuming that Elder's human subjects had thresholds equal to those of Sivian and White (1933).

2- Subjects pressed a key when a tone was audible and released it when inaudible. Free-field sound stimulation (MAF) with one ear plugged using a method of limits. Two sec tones. Means over nine subjects.

3- Based on large data set using TDH-39 earphone with a MX41/AR ear cushion, calibrated in a 9-A coupler.

4- This study measured the upper frequency hearing limit in 90 humans of different ages and five chimpanzees. The tone frequency just detected at 80 dB SPL was measured. Animals were trained to press a button in the presence of a tone in order to receive a food reward. Method of limits. Incorrect responses were punished with shock. The same headphones were used for chimpanzees and humans (#5 below).

5- Same methods as #4 above on 90 humans. The human threshold is the mean for a group of 15 subjects from 20 to 24 years of age. Subjects pressed a button when they heard a tone through earphones (method of limits).

6-7- These are measures comparing humans and chimpanzees in the upper frequency limit of hearing. The vertical lines plotted represent the median frequency (of three subjects) above which sound could not be detected. The intensity of the signals were high but unspecified. Methods as in #1 above. Earphones were used.

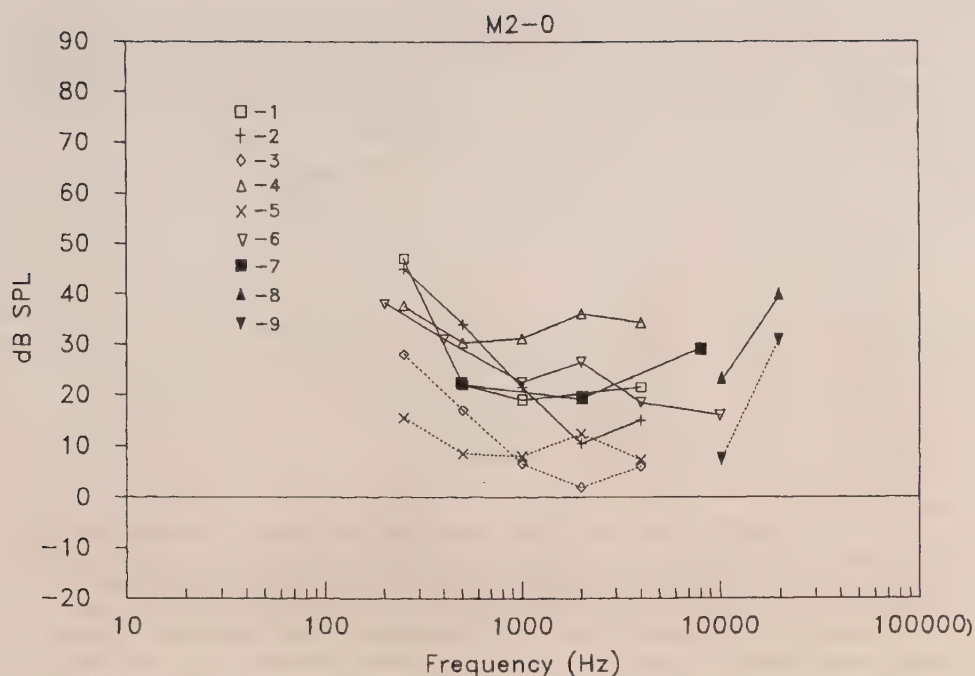


Fig. M2-0. Audiograms for *Homo sapiens* - human infants compared with adults tested in the same way.

- 1- 3 month old infants
- 2- 6 month old infants
- 3- adults
(Olsho, 1986)
- 4- 7-11 month old infants
- 5- adults
(Sinnott, Pisoni, and Aslin, 1983)
- 6- 6 month old infants (Trehub, Schneider, and Endman, 1980)
- 7- 6 month old infants (Berg and Smith, 1983)
- 8- 6 month old infants
- 9- adults
(Schneider, Trehub, and Bull, 1980)

References:

- Berg, K.M., and Smith, M.C. (1983) Behavioral thresholds for tones during infancy. *J. Exp. Child Psychol.* 35, 409-425.
- Olsho, L.W. (1986) Early development of human frequency resolution. In T. van der Water, E. Rubel, and R. Ruben (eds), *Biology of Change in Otolaryngology*. Elsevier: Amsterdam.
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Table M2-0. Audiograms for human infants compared with adults tested in the same way.

Frequency (Hz)	dB SPL								
	1	2	3	4	5	6	7	8	9
200						38			
250	47	45	28	37.7	15.5				
400						31			
500	22	34	17	30.3	8.5		22.8		
1000	19	21.5	6.5	31.2	8	22.5			
2000		10.5	2	36.1	12.4	26.5	19.6		
4000	21.5	15	6	34.3	7.3	18.5			
8000							28.5		
10000						16		23	7
19000								40	31.3

Notes:

1-3- Operant response for a visual reward using the method of constant stimuli. Infant was rewarded for some response (usually a head-turn) in the presence of a signal with the chance to watch an illuminated motorized toy. An observer decided on any given trial whether the infant responded using whatever criteria the observer could use. The reward to the infant followed the correct detection by the observer. Adults were tested similarly. Signals were 500 msec tone bursts repeated once per sec with 10 msec rise/fall times delivered to the right ear over headphones. Means: N=6 (adults), N=43 3-month olds, N=61 6-month olds.

4-5- Go, no-go operant head-turn for a visual reward using a tracking procedure. An observer decided whether or not the infant responded with a head-turn. Signals were one sec in duration with 20 msec rise/fall times. Free field. Means: N=9 adults, N=27 7.2-11 month olds.

6- Same methods as #4-5 above except that octave-band noises were used instead of tones, and the method of constant stimuli was used. Threshold was defined as 65% correct response. Means: N=14 to 18. Each subject was tested at only one or two frequencies.

7- Same methods as #4-5 above except that tone bursts were 250 msec repeated twice per sec. Earphones were used. The infant thresholds were described as being about 10 dB above human adults tested similarly. This paper also reports thresholds for 10, 14, and 18 month-old infants in a free sound field as well as with earphones (not shown here). Means: N=46.

8-9- Same methods as #4-5. Signals were half-octave noise bands with 25 msec rise/fall times. Means: N=32 infants.

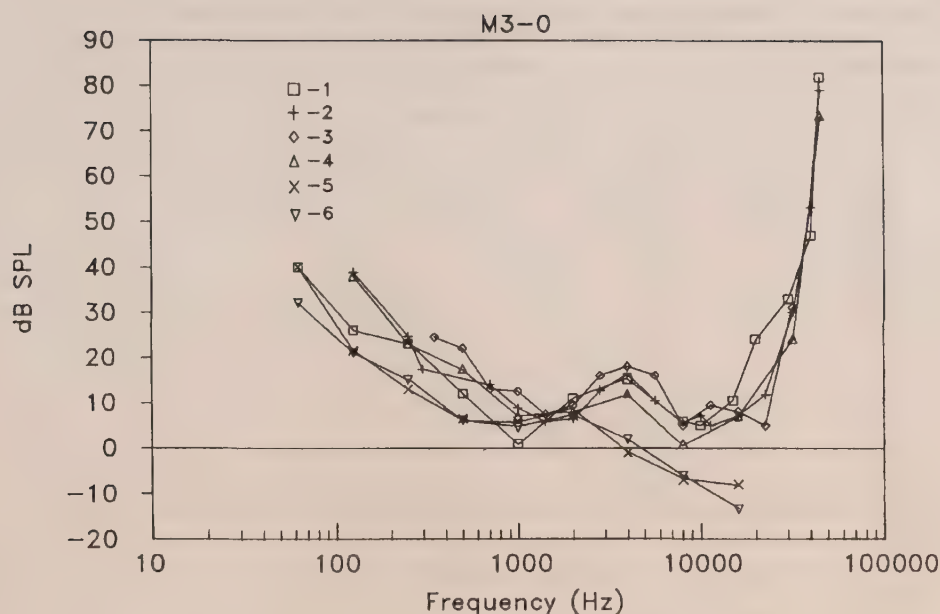


Fig. M3-0. Audiograms for several monkeys of the genus *Macaca*.

- 1- *Macaca irus* (or *M. fascicularis* or *M. cynomolgus*) - crab-eating macaque
Macaca nemestrina - pig-tailed macaque (Stebbins, Green, and Miller, 1966)
- 2- *Macaca mulatta* - rhesus monkey (Pfingst, Laycock, Flammino, Lonsbury-Martin, and Martin, 1978)
- 3- *Macaca mulatta* - rhesus monkey (Lonsbury-Martin and Martin, 1981)
- 4- *Macaca mulatta* - rhesus monkey (Pfingst, Hienz, and Miller, 1975)
- 5- *Macaca* sp. - macaque monkey, shock-Avoidance (Fujita and Elliot, 1965)
- 6- *Macaca* sp. - macaque monkey, reward (Fujita and Elliot, 1965)

References:

- Fujita, S., and Elliot, D.N. (1965) Thresholds of audition for three species of monkeys. *J. Acoust. Soc. Amer.* 37, 139-144.
- Lonsbury-Martin, B., and Martin, G. (1981) Effects of Moderately intense sound on auditory sensitivity in rhesus monkeys: Behavioral and neural observations. *J. Neurophysiol.* 46, 563-586.
- Pfingst, B.E., Hienz, R., and Miller, J. (1975) Reaction-time procedure for measurement of hearing. II. Threshold functions. *J. Acoust. Soc. Amer.* 57, 431-436.
- Pfingst, B.J., Laycock, J., Flammino, F., Lonsbury-Martin, B., and Martin, G. (1978) Pure tone thresholds for the Rhesus monkey. *Hear. Res.* 1, 43-47.
- Stebbins, W.C., Green, S., and Miller, F.L. (1966) Auditory sensitivity in the monkey. *Science* 153, 1646-1647.

Table M3-0. Audiograms for several monkeys of the genus *Macaca*.

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
62.5	40				40	32
125	26	38.9		38	21.5	21
250	23	24.6		23	13	15
300		17.4				
350			24.5			
500	12		22	17.5	6.5	6.2
707		14	13			
1000	1	8.9	12.5	7	6	4.5
1414		5.8	7.5			
2000	11	6.5	9.5	8	7	6.8
2828		12.7	16			
4000	15	16.3	18	12	-1	2
5657		10.5	16			
8000	6	5.7	5	1	-7	-6
10000	5	7.2				
11314		5	9.5			
15000	10.5					
16000		7	8	7	-8	-13.5
20000	24					
22628		11.8	5			
30000	33					
32000		30	31	24		
40000	47	53.1				
45000	82			73.5		
45256		79.2				

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli. Animals trained to press a key to initiate a three sec tone signal with a given probability. A response on a second key during the tone presentation was rewarded and constituted a "hit." Headphones were used. Medians of four animals.

2- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to depress a key ("observing response") which produced a tone presentation within a variable time. Releasing the key within 1 sec of tone onset was scored as a "hit." Headphones were used. Means of 13 animals.

3- Operant conditioning for a food reward using the method of constant stimuli. Same procedures as #2 above. A single earphone was used. Means of six animals.

4- Operant conditioning for a food reward using the method of constant stimuli. Same procedures as #2 above. A single earphone was used. Means of two animals.

5- Instrumental shock-avoidance conditioning (bar press) using a modified method of limits. Signals were 200 msec bursts presented twice per sec with 100 msec rise/fall times. Data are means over four animals.

6- Operant conditioning for a food reward using a modified method of limits. Animals were trained to press a bar once in the presence of a tone to receive food. Signals were 200 msec bursts presented twice per sec with 100 msec rise/fall times. Data are means over two animals.

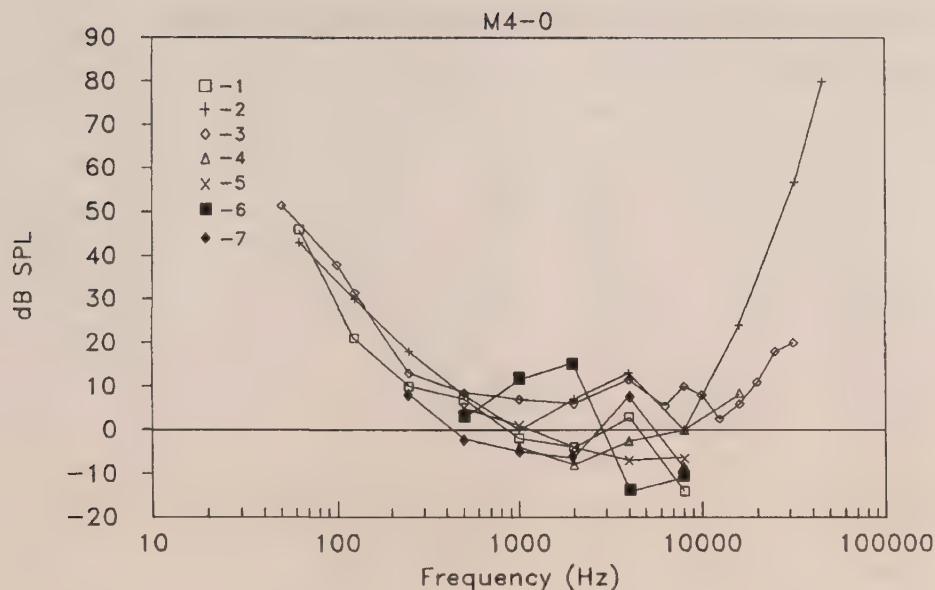


Fig. M4-0. Audiograms for several monkeys of the Genus *Macaca*.

- 1- Harris (1943)
- 2- Stebbins (1973)
- 3- Behar, Cronholm, and Loeb (1965)
- 4- Clack and Herman (1963)
- 5- Dalton, Taylor, Henton, and Allen (1969)
- 6- Dalton (1968)
- 7- Clack (1966)

References:

- Behar, I., Cronholm, J.N., and Loeb, M. (1965) Auditory Sensitivity of the rhesus monkey. *J. Comp. Physiol. Psychol.* 59, 426-433.
- Clack, T.D. (1966) Effect of signal duration on the auditory sensitivity of humans and monkeys (*Macaca mulatta*). *J. Acoust. Soc. Amer.* 40, 1140-1146.
- Clack, T.D., and Herman, P.N. (1963) A single-lever psychophysical adjustment procedure for measuring auditory thresholds in the monkey. *J. Aud. Res.* 3, 175-183.
- Dalton, L.W. (1968) Auditory sensitivity in the rhesus (*Macaca mulatta*) and the white-throated capuchin (*Cebus capuchinus*) monkeys: A comparison of three techniques. 6571st Aeromedical Research Laboratory Final Report, ARL-TR-68-14, pp. 1-55.
- Dalton, L.W., Taylor, H., Henton, W., and Allen, J.N. (1969) Auditory thresholds in the rhesus monkey using a closed-system helmet. *J. Aud. Res.* 9, 178-182.
- Harris, J.D. (1943) The auditory acuity of preadolescent monkeys. *J. Comp. Psychol.* 35, 255-265.
- Stebbins, W.C. (1973) Hearing of Old World monkeys (*Cercopithecinae*). *American J. of Physical Anthropology* 38, 357-364.

Table M4-0. Audiograms for several monkeys of the Genus *Macaca*.

Frequency (Hz)	dB SPL						
	1	2	3	4	5	6	7
50			51.5				
62.5	46	43					
100			38				
125	21	30	31.5				
250	10	18	13				8
500	7	8	8.5		5	4	-2.3
1000	-2	0	7	-4	1	10.2	-5.5
2000	-4	7	6	-8	-4	13.1	-6
4000	3	13	11.5	-2.5	-7	-13.3	7
6300			5.5				
8000	-14	0	10	0	-6.5	-11	-9
10000			8				
12500			2.5				
16000		24	6	8.5			
20000			11				
25000			18				
31500			20				
32000		57					
45000		80					

Notes:

1- Instrumental shock-avoidance using a modified method of limits. Animals in a small cage were required to move slightly in the presence of a tone in order to avoid shock. Movement of the cage was detected using a stabilimeter. Free-field sound stimulation. Data are means over eight animals. These were two *M. mulatta*, three *M. rhesus* (*M. mulatta*?), two *M. sinica*, and one macaque of indeterminate species.

2- Operant conditioning for a food reward using using a tracking psychophysical procedure. Animals were trained to contact a manipulandum (observing response) and to release when the signal was detected. Earphones were used.

This paper reports a "representative" audiogram for seven species (four genera) of Cercopithecinae subfamily of Old World monkeys (Cercopithecidae). The species are: *Macaca arctoides*, *Macaca fascicularis*, *Macaca mulatta*, *Macaca nemestrina*, *Cercopithecus aethiops*, *Erythrocebus patas*, and *Papio papio*.

3- Instrumental shock-avoidance conditioning using a tracking psychophysical procedure. Animals were trained to press a lever in the presence of a tone in order to avoid shock. Free-field sound stimulation. Signals were tones with 100 msec rise/fall times. Data are means of four animals.

4- Instrumental shock-avoidance conditioning using a tracking procedure. Animals were trained to press a lever in the presence of a tone in order to avoid shock. Free-field sound stimulation. Signals had 10 msec rise/fall times. Means over six animals.

5- Classically conditioned suppression of an operant response using the method of constant stimuli. Animals were trained to lever-press on a VI 90-sec schedule. A tone presentation signalled impending shock and suppressed operant responding. Data are medians over four animals (*Macaca mulatta*).

6- Conditioned suppression as described above for #5. Data are means over two animals (*Macaca mulatta*).

7- Same as #4. Most sensitive ear of two *Macaca mulatta* shown for 1 to 8 kHz, and four ears in two animals shown for .25 to 1 kHz. Earphones were used. Minimum audible field thresholds also given (not plotted here) and show less of a "4-kHz notch" than the earphone thresholds.

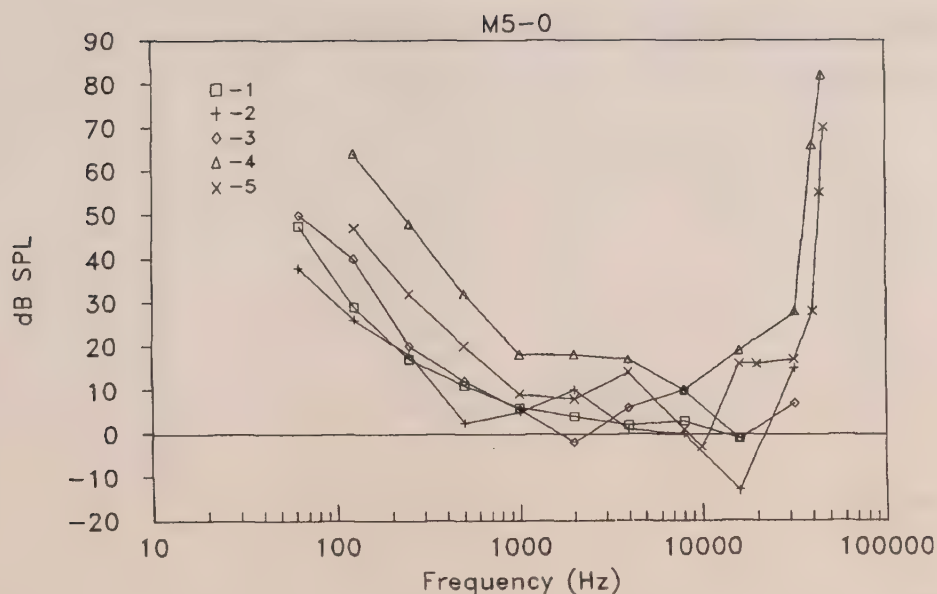


Fig. M5-0. Audiograms for *Saimiri sciureus* (squirrel monkey).

- 1- Fujita and Elliot, 1965, bar press to obtain food
- 2- Fujita and Elliot, 1965, bar press to avoid shock
- 3- Fujita and Elliot, 1965, double grill box
- 4- Green, 1975
- 5- Beecher, 1974a

References:

- Beecher, M. (1974a) Pure tone thresholds of the squirrel monkey (*Saimiri sciureus*). J. Acoust. Soc. Amer. 55, 196-198.
- Fujita, S., and Elliot, D.N. (1965) Thresholds of audition for three species of monkeys. J. Acoust. Soc. Amer. 37, 139-144.
- Green, S. (1975) Auditory sensitivity and equal loudness in the squirrel monkey (*Saimiri sciureus*). J. Exp. Anal. Behav. 23, 255-264.

Table M5-0. Audiograms for *Saimiri sciureus* (squirrel monkey).

Frequency (Hz)	dB SPL				
	1	2	3	4	5
62.5	47.5	38	50		
125	29	26	40	64	47
250	17	18	20	48	32
500	11	2.5	12	32	20
1000	6	5	5.5	18	9
2000	4	10	-2	18	8
4000	2	1	6	17	14
8000	3	0	10	10	1
10000					-3
16000	-1	-13	-1	19	16
20000					16
32000		15	7	28	17
40000				66	28
44000					55
45000				82	
46000					70

Notes:

1- Operant conditioning for a food reward using a modified method of limits. Animals were trained to press a bar once in the presence of a tone to receive food. Signals were 200 msec bursts presented twice per sec with 100 msec rise/fall times. Free-field sound stimulation. Data are means over two animals.

2- Instrumental shock-avoidance conditioning (bar press) using a modified method of limits. Signals were 200 msec bursts presented twice per sec with 100 msec rise/fall times. Free-field sound stimulation. Data are means over two animals.

3- Instrumental shock-avoidance in a double grill box using a modified method of limits. Animals were trained to cross a barrier in the presence of a tone in order to avoid shock. Signals were 200 msec bursts presented twice per sec with 100 msec rise/fall times. Free-field sound stimulation. Data are means over five animals.

4- Instrumental shock-avoidance using the method of constant stimuli. Animals were trained to hold down a bar (initiating a tone signal within a certain time), and then to release the bar in the presence of the tone in order to avoid shock. Signals delivered through earphones had 10 msec rise/fall times. Data are means over four animals.

This paper also reported thresholds on two animals using appetitive conditioning. The results from this procedure did not differ in important ways from the avoidance data shown here.

5- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to lick a feeding tube to initiate a trial, and then to press a lever in the presence of a tone in order to receive food. Free-field sound presentation. Signals were tones of 200 msec duration and with 25 msec rise/fall times. Data are means over two animals.

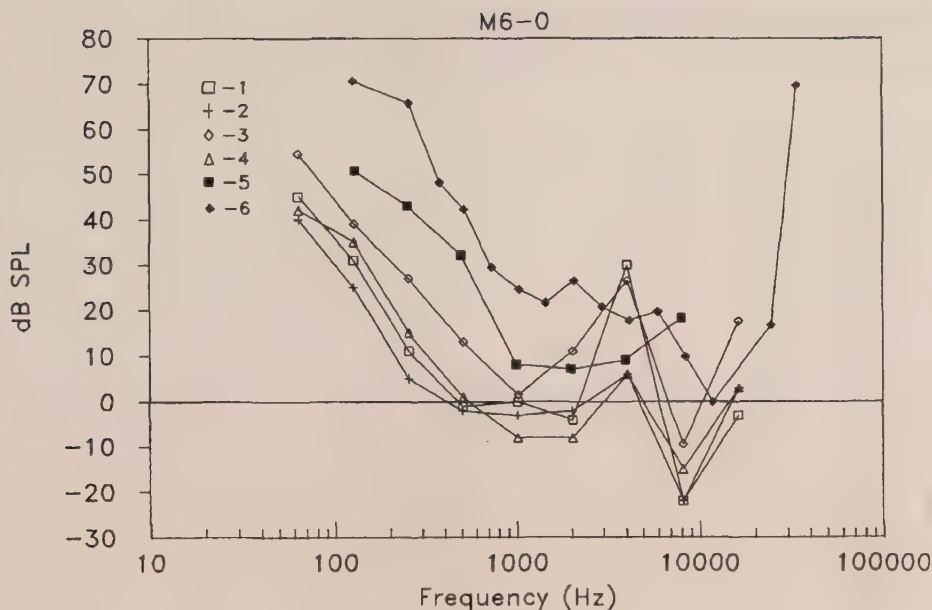


Fig. M6-0. Audiograms for six monkey species.

- 1- *Papio anubis* - baboon (Wendt, 1934)
- 2- *Macaca rhesus* - Likely *M. mulatta* - rhesus monkey (Wendt, 1934)
- 3- *Ateles ater* - spider monkey (Wendt, 1934)
- 4- *Cercocebus torquatus* - a mangabey (Wendt, 1934)
- 5- *Macaca nemestrina* - pig-tailed macaque (Semenoff and Young, 1964)
- 6- *Erythrocebus patas* - patas monkey (Smith, Moody, Stebbins, and Norat (1987)

References:

- Semenoff, W.A. and Young, F.A. (1964) Comparison of the auditory acuity of man and monkey. *J. Comp. Physiol. Psychol.* 57, 89-93.
- Smith, D.W., Moody, D.B., Stebbins, W.C., and Norat, M.A. (1987) Effects of outer hair cell loss on the frequency selectivity of the patas monkey auditory system. *Hear. Res.* 29, 125-138.
- Wendt, G.R. (1934) Auditory acuity in the monkey. *Comp. Psychol. Monograph* 10, 1-51.

Table M6-0. Audiograms for six monkey species.

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
64	45	40	54.5	42		
128	31	25	39	35		
125						72
130					50.5	
250					42.8	67
256	11	5	27	15		
370						49
500					32	43
512	-1	-2	13	1		
715						30
1000					8	25
1024	0	-3	1.5	-8		
1400						22
2000					7	27
2048	-4	-2	11	-8		
2850						21
4000					9	18
4096	30	6	26.5	6		
5700						20
8000					10	10
8192	-22	-22	-9.5	-15		
11200						0
16384	-3	3	17.5	3		
23000						17
32000						71

Notes:

1-4- Operant conditioning for a food reward using a descending method of limits. Animals were trained to open a drawer in the presence of a tone. Free-field tones with 50 msec rise/fall times. Human subjects were tested similarly. Monkey thresholds (in dB attenuation of signal to the loudspeaker) were expressed relative to the human thresholds. Data plotted are the differences between monkeys and humans added to human thresholds as determined by Sivian and White (1933). The assumptions of this "calibration" are that the human subjects are identical to Sivian and White's in threshold, and that the sound field at the human and monkey ears are the same.

Study reports reaction times as a function of signal level, many psychometric functions, and an analysis of false alarms. Data are for one individual of each species except for the squirrel monkey where the data are means over two animals.

5- Classically conditioned galvanic skin response (GSR) using the ascending method of limits. Animals were restrained with GSR recording electrodes on the first two fingers of both hands, and the shock electrode on the right forearm. Earphones were used. Absolute sound pressure calibrations were not made. Three human subjects were tested using the same earphones and instructed to press a key upon tone presentation. The monkeys thresholds were presented relative to the human thresholds. The thresholds are plotted here under the assumption that the sensitivity of the human subjects could be described by the data of Sivian and White (1933).

6- Operant conditioning for a food reward using tracking. Animals were trained to make an observing response, and then to release during the 2.5 sec (5 msec rise/fall times) tone. Earphones were used. Means: N=4.

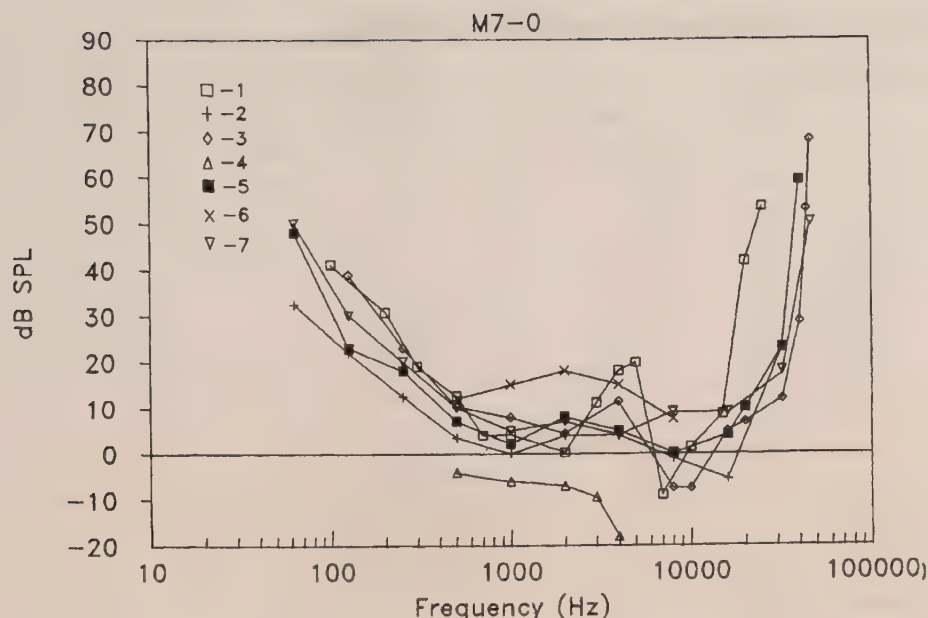


Fig. M7-0. Audiograms for several monkey species.

- 1- *Hapale jacchus* (*Callithrix jacchus*) - marmoset (Seiden, 1957)
- 2- *Macaca cynomolgus* - crab-eating macaque (Fujita and Elliot, 1965)
- 3- *Aotus trivirgatus* - owl monkey (Beecher, 1974b)
- 4- *Cebus capucinus* - white-throated capuchin (Bragg and Dreher, 1969)
- 5- *Papio cynocephalus* - yellow baboon (Hienz, Turkkan, and Harris, 1982)
- 6- *Cebus capucinus* - white-throated capuchin (Dalton, 1968)
- 7- *Cercopithecus mitis* - blue monkey (Brown and Waser, 1984)

References:

- Beecher, M. (1974b) Hearing in the owl monkey (*Aotus trivirgatus*): Auditory sensitivity. *J. Comp. Physiol. Psychol.* 86, 598- 901.
- Bragg, V.C., and Dreher, D.E. (1969) A shock-avoidance technique for determining audiologic thresholds in the Cebus monkey. *J. Aud. Res.* 3, 270-277.
- Brown, C.H., and Waser, P.M. (1984) Hearing and communication in blue monkeys (*Cercopithecus mitis*). *Anim. Behav.* 32, 66-75.
- Dalton, L.W. (1968) Auditory sensitivity in the rhesus (*Macaca mulatta*) and the white-throated capuchin (*Cebus capucinus*) monkeys: A comparison of three techniques. 6571st Aeromedical Research Laboratory Final Report, ARL-TR-68-14, pp. 1-55.
- Fujita, S., and Elliot, D.N. (1965) Thresholds of audition for three species of monkeys. *J. Acoust. Soc. Amer.* 37, 139-144.
- Hienz, R.D., Turkkan, J.S., and Harris, A.H. (1982) Pure tone thresholds in the yellow baboon (*Papio cynocephalus*). *Hear. Res.* 8, 71-76.
- Seiden, H.R. (1957) Auditory acuity of the marmoset monkey (*Hapale jacchus*). Unpublished Doctoral Dissertation, Princeton University.

Table M7-0. Audiograms for several monkey species.

Frequency (Hz)	1	2	3	dB SPL	4	5	6	7
62.5		32.5				48		50
100	41.2							
125		22	39			23		30
200	30.8							
250		12.5	23			18		20
300	19.1							
500	12.7	3.5	10.5	-4		7	12	10
700	4.1							
1000	4.2	0	8	-6		2	15	5
2000	0.3	4	4.5	-7		8	18	7
3000	11.2			-9.5				
4000	18.2	4	11.5	-18		5	15	4
5000	19.9							
7000	-9							
8000		-1	-7.5			0	7.5	9
10000	1.5		-7.5					
15000	8.7							
16000		-5.5	5			4		9
20000	41.8		7			10		
25000	53.5							
32000		23	12			23		18
40000			28.7			59		
44000			53					
46000			68					50

Notes:

1- Instrumental shock-avoidance (double grill box) using the method of limits. Signals were free-field tones. Data are means over five animals.

2- For three animals, instrumental shock-avoidance conditioning (bar press) using a modified method of limits. For two animals, operant conditioning for a food reward using a modified method of limits. Animals were trained to press a bar once in the presence of a tone to receive food. Signals were 200 msec bursts presented twice per sec with 100 msec rise/fall times. Data are means over all five animals.

3- Operant conditioning for a food reward using a tracking procedure. Animals were trained to lick a spout to initiate a tone presentation, and then to pull a lever in the presence of a tone in order to receive food reward. Free-field signals were 200 msec tone bursts with 25 msec rise/fall times. Data are means over two animals.

4- Instrumental shock-avoidance (pressing a panel) using a method of limits. Earphones were used. Data are means over 14 animals.

5- Operant conditioning for a food reward using the method of constant stimuli. Animals trained to press and hold a lever to initiate a trial, and to release the lever within 1.5 sec after tone onset. Data are means over four animals.

6- Classical conditioning of the galvanic skin response (GSR) to shock using the method of limits. Animals were restrained with shock electrodes on one foot and GSR electrode on the other foot. Data are means over four animals.

7- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to press and hold a response key to initiate a trial, and then to release the key within two sec after tone onset. Signals had 100 msec rise/fall times. Free-field stimulation. Data are means over two animals.

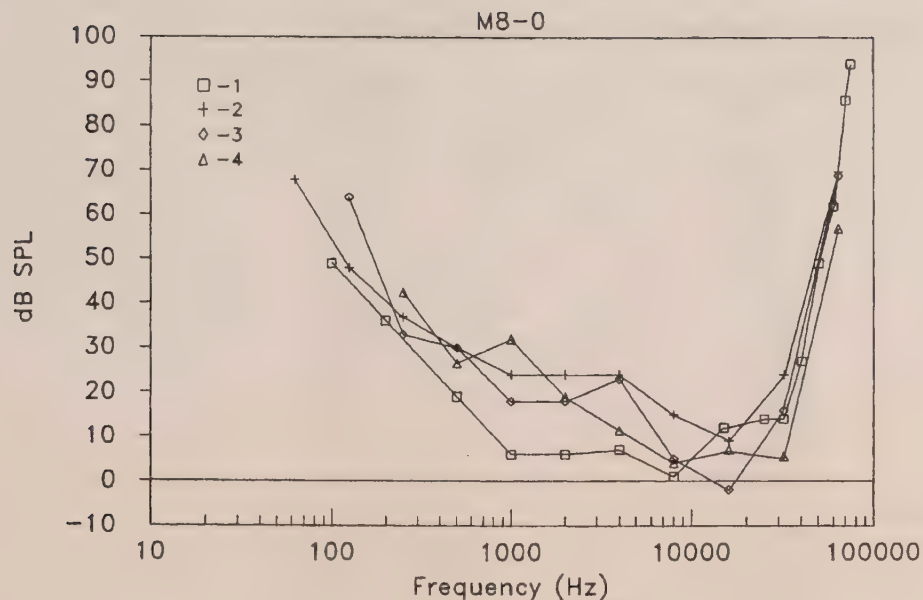


Fig. M8-0. Audiograms for several prosimians.

- 1- *Lemur sp.* - lemur (Mitchell, Vernon, and Herman, 1971; Gillette, Brown, Herman, Vernon, and Vernon, 1973)
- 2- *Nycticebus coucang* - slow loris (Heffner and Masterton, 1970)
- 3- *Perodicticus potto* - potto (Heffner and Masterton, 1970)
- 4- *Galago senegalensis* - bushbaby (Heffner, Ravizza, and Masterton, 1969)

References:

- Mitchell, C., Vernon, J., and Herman, P. (1971) What does the lemur really hear? *J. Acoust. Soc. Amer.* 50, 710-711.
- Heffner, H., and Masterton, B. (1970) Hearing in primitive primates: Slow loris (*Nycticebus coucang*) and potto (*Perodicticus potto*). *J. Comp. Physiol. Psychol.* 71, 175-182.
- Heffner, H., Ravizza, R.J., and Masterton, B. (1969b) Hearing in Primitive mammals IV: Bushbaby (*Galago senegalensis*). *J. Aud. Res.* 9-19-23.
- Gillette, R.G., Brown, R., Herman, P., Vernon, S., and Vernon, J. (1973) The auditory sensitivity of the lemur. *Amer. J. Phys. Anthro.* 38, 365-370.

Table M8-0. Audiograms for several prosimians.

Frequency (Hz)	dB SPL			
	1	2	3	4
62.5		68		
100	49			
125		48	64	
200	36			
250		37	33	42.5
500	19	30	30	26.5
1000	6	24	18	32
2000	6	24	18	19
4000	7	24	23	11.5
8000	1	15	5	4
15000	12			
16000		9	-2	7
25000	14			
32000	14	24	16	5.5
40000	27			
50000	49			
60000	62			
64000		70	69	57
70000	86			
75000	94			

Notes:

1- Instrumental shock-avoidance conditioning using the method of constant stimuli. Animals were trained to press a lever in the presence of a tone in order to avoid shock. Free-field sound stimulation.

These thresholds are from Figure 1 in Gillette et al (1973) which displays the combined results from that study and an earlier one (Mitchell et al, 1971). Note that the latter study followed an original paper (Mitchell, Gillette, Vernon, and Herman, 1970) on lemur hearing. The thresholds in this paper seemed rather high and motivated the study by Mitchell et al (1971) which employed a different behavioral technique to obtain generally lower thresholds.

Data are means over five animals from Mitchell et al (1971) and four animals from Gillette et al (1973). Three of the animals were used in both studies.

The Mitchell et al (1970) study used three lemur species: *L. catus*, *L. macaco fulvus*, and *L. macaco*. The results showed no important differences between them in auditory sensitivity. The Mitchell et al (1971) and the Gillette et al (1973) studies used only *Lemur catus* (ringtailed lemur).

2- Classically conditioned suppression of licking using the method of constant stimuli. Animals were trained to lick a water spout to obtain food. A tone signal presentation signalled impending shock, and suppresses the operant licking response. Free-field sound presentation. Signals were tones with 25 msec rise/fall times (except below 500 Hz where the rise/fall times occurred during 10 full cycles of the tone). Data are means over two animals.

3- Same as #2.

4- Same as #2.

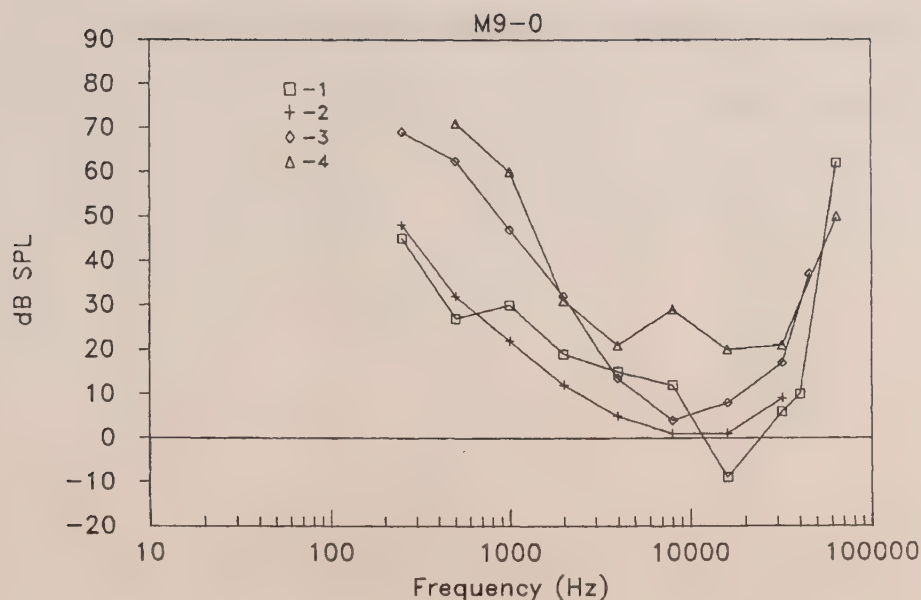


Fig. M9-0. Audiograms for a prosimian and two primitive mammals.

- 1- *Tupaia glis* - tree shrew (Heffner, Ravizza, and Masterton, 1969)
conditioned suppression
- 2- *Tupaia glis* - tree shrew (Heffner, Ravizza, and Masterton, 1969)
avoidance conditioning
- 3- *Hemiechinus auritus* - hedgehog (Ravizza, Heffner, and Masterton, 1969a)
- 4- *Didelphis virginianus* - opossum (Ravizza, Heffner, and Masterton, 1969b)

References:

- Heffner, H.E., Ravizza, R.J., and Masterton, B. (1969a) Hearing in primitive mammals: III Tree shrew (*Tupaia glis*). J. Aud. Res. 9, 12-18.
- Ravizza, R., Heffner, H., and Masterton, B. (1969a) Hearing in primitive mammals I: Opossum (*Didelphis virginianus*). J. Aud. Res. 9, 1-7.
- Ravizza, R., Heffner, H., and Masterton, B. (1969b) Hearing in primitive mammals II: Hedgehog (*Hemiechinus auritus*). J. Aud. Res. 9, 8-11.

Table M9-0. Audiograms for a prosimian and two primitive mammals.

Frequency (Hz)	dB SPL			
	1	2	3	4
250	45	48	69	
500	27	32	62.5	71
1000	30	22	47	60
2000	19	12	32	31
4000	15	5	13.5	21
8000	12	1	4	29
16000	-9	1	8	20
32000	6	9	17	21
40000	10			
45000			37	
64000	62			50

Notes:

1- Classically conditioned suppression of an operant response using the method of constant stimuli. Animals were trained to lick a drinking tube in order to obtain a food reward on a variable ratio schedule. During this ongoing behavior, tone presentations signalled impending shock, and eventually caused the temporary cessation of operant licking. Data are means over two animals.

2- Instrumental shock-avoidance in a double grill box using a method of constant stimuli. Animals were trained to cross a hurdle in the presence of a tone in order to avoid shock. Data are means over two animals.

3- Same methods as #1. Data are means over two animals.

4- Same methods as #1. Data are means over two animals.

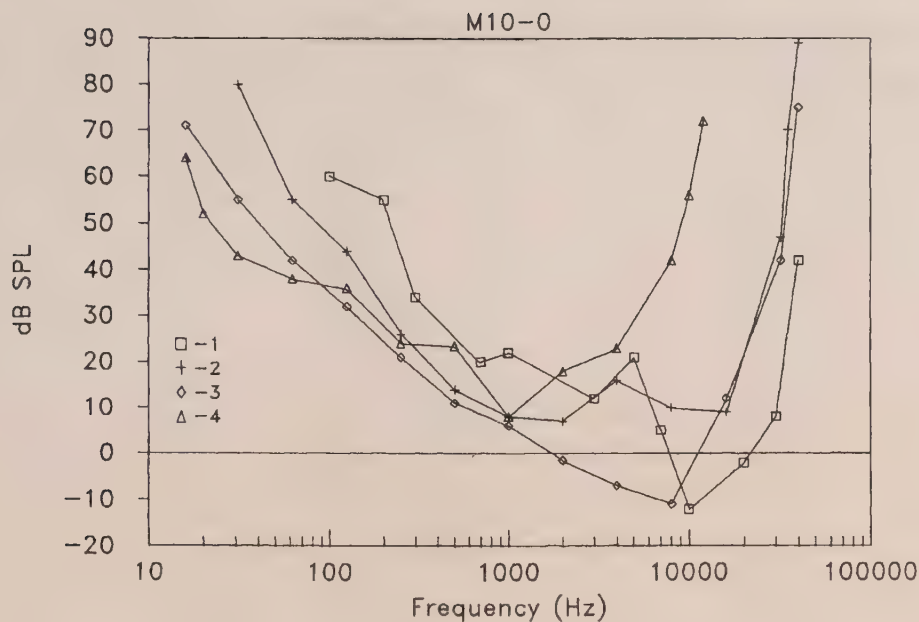


Fig. M10-0. Audiograms for several large mammals.

- 1- *Ovis aries* - sheep (Wollack, 1963)
- 2- *Equus caballus* - horse (Heffner and Heffner, 1983)
- 3- *Bos taurus* - cattle (Heffner and Heffner, 1983)
- 4- *Elephas maximus* - Indian elephant (Heffner and Heffner, 1982)

References:

- Heffner, R.S., and Heffner, H.E. (1982) Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Psychol.* 96, 926-944.
- Heffner, R.S., and Heffner, H.E. (1983) Hearing in large mammals: Horses (*Equus caballus*) and cattle (*Bos taurus*). *Behav. Neurosci.* 97, 299-309.
- Wollack, C.H. (1963) The auditory acuity of the sheep (*Ovis aries*) *J. Aud. Res.* 3, 121-132.

Table M10-0. Audiograms for several large mammals.

Frequency (Hz)	dB SPL			
	1	2	3	4
16			71	64
20				52
31		80	55	43
62		55	42	38
100	60			
125		44	32	36
200	55			
250		26	21	24
300	34			
500		14	11	23.5
700	20			
1000	22	8	6	8
2000		7	-1.5	18
3000	12			
4000		16	-7	23
5000	21			
7000	5			
8000		10	-11	42
10000	-12			56
12000				72
16000		9	12	
20000	-2			
30000	8			
32000		47	42	
35000		70		
40000	32	42	89	

Notes:

1- Instrumental shock-avoidance using a modified method of limits. Animal trained to lift a leg in the presence of a tone signal in order to avoid shock. Signals were 2.75 sec tones with 5 msec rise/fall times. Free-field sound stimulation. Data are means over three animals.

2- Operant conditioning with a water reward using a tracking procedure. Animal trained to place its nose on a plate which initiated a tone signal. Within 3 sec of tone onset, the animal could break contact with the observing plate and make contact with a second plate in order to gain brief access to water. Signals were free-field tones with rise/fall times of 20 msec (for frequencies above 125 Hz), or longer for the lower frequencies. Data are means over three animals (quarter horse gelding, Appaloosa mare, and Welch pony x quarter horse gelding).

3- Same as #2. Data are means over two polled Hereford cows.

4- Operant conditioning with a fruit-flavored sugar solution reward using a method of constant stimuli. Signals were free-field tones with 20 msec rise/fall times for frequencies above 500 Hz, and longer times for the lower frequencies. Data are for one animal (7-yr-old female Indian elephant).

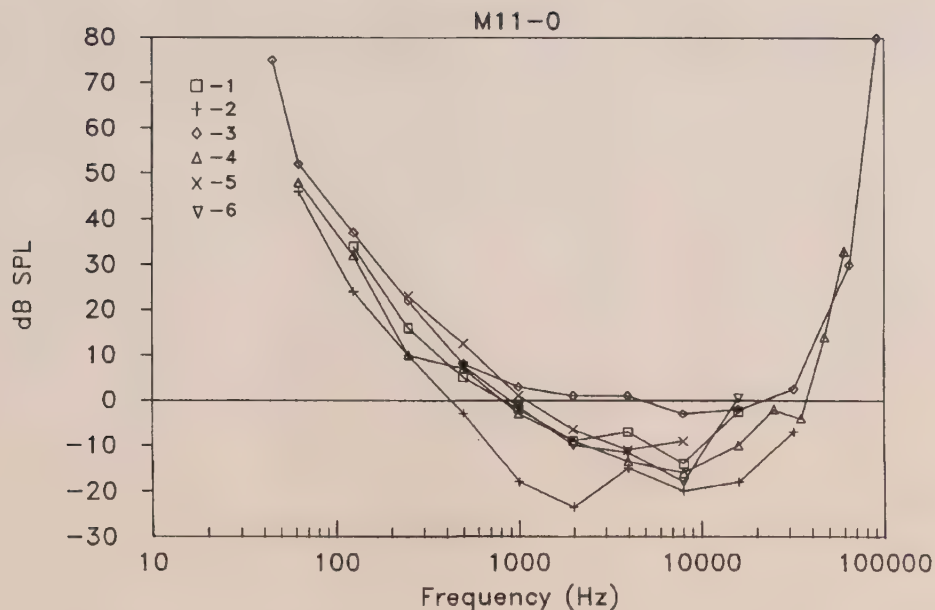


Fig. M11-0. Audiograms for *Felis catus* (cat).

- 1- Costalupes (1983)
- 2- Elliot, Stein, and Harrison (1960)
- 3- Heffner and Heffner (1985a)
- 4- Neff and Hind (1955)
- 5- Gerken and Sandlin (1977)
- 6- Gerken, Saunders, Simhadri-Sumithra, and Bhat (1985)

References:

- Costalupes, J. (1983) Temporal integration of pure tones in the cat. *Hear. Res.* 9, 43-54.
- Elliot, D., Stein, L., and Harrison, M. (1960) Determination of absolute-intensity thresholds and frequency difference thresholds in cats, *J. Acoust Soc. Amer.* 32, 380-384.
- Gerken, G.M. and Sandlin, D. (1977) Auditory reaction time and absolute threshold in cat. *J. Acoust. Soc. Amer.* 61, 602-607.
- Gerken, G.M., Saunders, S.S., Simhadri-Sumithra, R., and Bhat, K.H.V. (1985) Behavioral thresholds for electrical stimulation applied to auditory brainstem nuclei in cat are altered by injurious and noninjurious sound. *Hear. Res.* 20, 221-231.
- Heffner, R.S. and Heffner, H.E. (1985a) Hearing range of the domestic cat. *Hear. Res.* 19, 85-88.
- Neff, W. and Hind, J. (1955) Auditory thresholds of the cat. *J. Acoust Soc. Amer.* 27, 480-483.

Table M11-0. Audiograms for *Felis catus* (cat).

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
45			75			
62.5		46	52	48		
125	34	24	37	32		
250	16	10	22	10	23	
500	5	-3	8	7	12.5	7.5
1000	-2	-18	3	-3	1	-1.5
2000	-9	-23.5	1	-9	-6.5	-10
4000	-7	-15	1	-13.5	-11	-11.5
8000	-14	-20	-3	-16	-9	-18
16000	-2.5	-18	-2	-10		0.5
25000				-2		
32000		-7	2.5			
35000				-4		
47000				14		
60000				33		
64000			30			
91000			80			

Notes:

1- Operant conditioning with a food reward using a tracking psychophysical procedure. A yoke-restrained cat was trained to initiate a trial by pressing and holding a response panel with its nose. A detection was defined as (and the animal was rewarded for) releasing the hold within 1 sec of stimulus onset. Signals were 500 msec tone bursts with 10 msec rise/fall times. Data are medians over three animals.

2- Instrumental shock-avoidance conditioning in a tilt-cage using the descending method of limits. Signals were continuous tones with 100 msec rise/fall times. Data are means over 8 animals.

3- Instrumental shock-avoidance using the method of constant stimuli. Water-deprived animals were trained to make steady contact with a drinking tube in order to obtain water. Breaking contact with the tube during the signal presentation was defined as a detection. Signals were 400 msec tone bursts pulsed on twice per sec with rise/fall times ranging from 100 msec at the lowest frequencies (31 and 45 Hz), and 10 msec for frequencies above 500 Hz. Data are medians over two animals.

4- Instrumental shock-avoidance conditioning in a tilt-cage using a method of limits. Signals were 4 sec tones with 500 msec rise/fall times. Data are averages over three animals.

5- Operant conditioning with a liquid food reward using a tracking psychophysical procedure. Animals were trained to initiate a trial by placing a paw into an opening. A detection was defined as (and the animals was rewarded for) removing the paw before a predetermined time from stimulus onset (1-9 sec random delays). Signals were 120 msec tone bursts with 20 msec rise/fall times. Data are means over two animals.

6- Operant conditioning with a liquid food reward using a tracking psychophysical procedure. Animals were trained to initiate a trial by placing a paw into an opening. A detection was defined as (and the animals was rewarded for) removing the paw within 1.1 sec of stimulus onset. Signals were 100 msec tone bursts with 10 msec rise/fall times, repeated 5 times. Data are means over three animals.

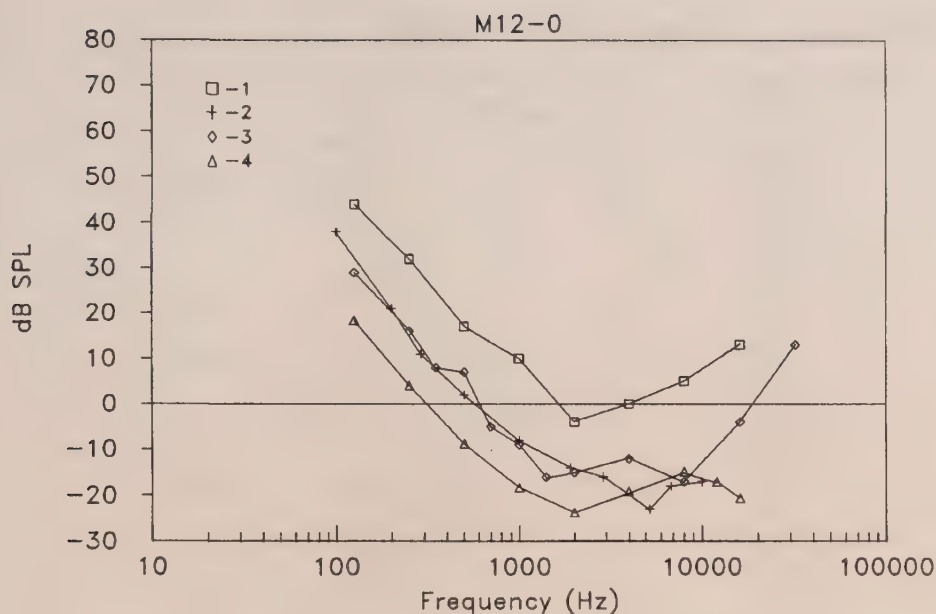


Fig. M12-0. Audiograms for *Felis catus* (cat).

- 1- Trahiotis and Elliot (1970)
- 2- McGill (1959)
- 3- Miller, Watson, and Covell (1963)
- 4- Sokolovski (1973)

References:

- McGill, T.E. (1959) Auditory sensitivity and the magnitude of cochlear potentials. *Ann. Otol. Rhinol. Laryngol.* 68, 193-207.
- Miller, J.D., Watson, C.S., and Covell, W.P. (1963) Deafening effects of noise on the cat. *Acta Oto-laryngol. Suppl.* 176, 1-81.
- Sokolovski, A. (1973) Normal threshold of hearing for cat for free-field listening. *Arch. Klin. Exp. Ohr., Nas.- u. Kehlk. Heilk.* 203, 232-240.
- Trahiotis, C., and Elliot, D.N. (1970) Behavioral investigation of some possible effects of sectioning the crossed olivocochlear bundle. *J. Acoust. Soc. Amer.* 47, 592-596.

Table M12-0. Audiograms for *Felis catus* (cat).

Frequency (Hz)	dB SPL			
	1	2	3	4
100		38		
125	44		29	18.4
200		21		
250	32		16	4
290		11		
350			8	
500	17	2	7	-8.7
700			-5	
1000	10	-8	-9	-18.3
1400			-16	
1900		-14		
2000	-4		-15	-23.7
2900		-16		
4000	0		-12	-19.2
5200		-23		
6800		-18		
8000	5		-17	-14.8
10000		-17		
12000				-17
16000	13		-4	-20.6
25000				
32000			13	

Notes:

1- Instrumental shock-avoidance in a double grill box using a modified method of limits psychophysical procedure.

Sectioning of the olivocochlear bundle caused no changes in absolute thresholds, caused slightly increased masking, and caused no change in temporary threshold shift caused by intense sound.

Signals were 500 msec tone bursts presented once every 0.8 sec with 50 msec rise/fall times. Average of six animals.

2- Operant conditioning with a food reward using a tracking psychophysical procedure. Animals were trained to sit at one end of a cage and, at the presentation of a tone, to cross a 6-inch high barrier and move to the other end of the cage for a reward. Signals were tones with 500 msec rise/fall times. Data are averages over four animals.

3- Instrumental shock-avoidance conditioning using a modified method of limits with a tracking component. Animals were trained to cross a hurdle in a double grill-cage in the presence of a tone signal in order to avoid shock. Signals were five, one-sec duration tone bursts with 100 msec rise/fall times with 500 msec silent intervals between them. Data are median thresholds over 34 cats except for the thresholds at 350, 700, and 1400 Hz where data are medians over eight of the 34 animals.

4- Operant conditioning for a food reward ("push-pull" conditioning technique) using the method of limits. Data are means over 19 animals, surgically deafened in one ear.

Note that there are additional data for two cats presented by Dworkin, Seymour, and Sutherland (1933) using operant conditioning for a food reward. However, since these thresholds lacked any absolute sound pressure calibration, they are not plotted here.

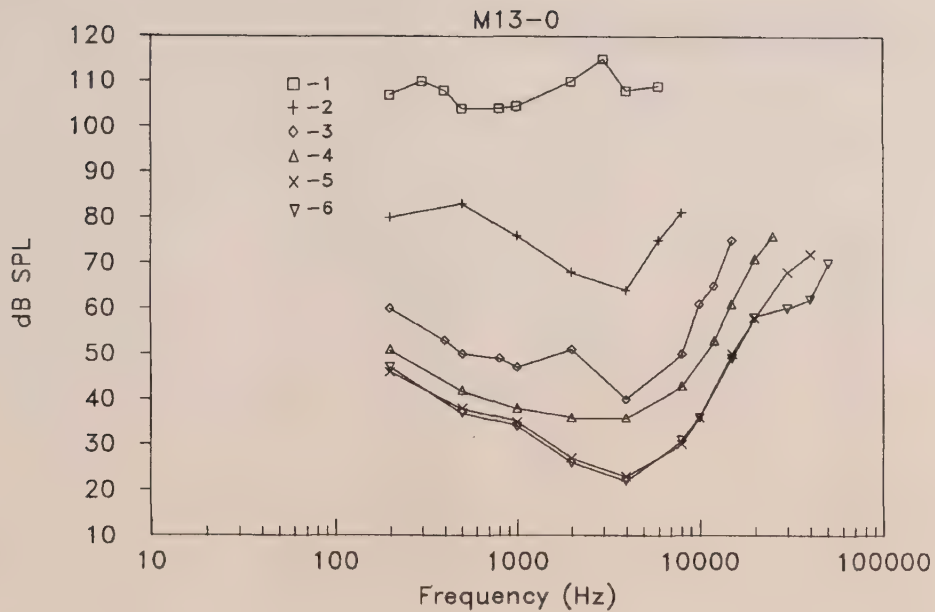


Fig. M13-0. Audiograms during the first 30 days of postnatal development of *Felis catus* (cat) (Ehret and Romand, 1981).

- 1- 6 days after birth
- 2- 10 days
- 3- 12 days
- 4- 15 days
- 5- 22 days
- 6- 30 days

Reference:

Ehret, G., and Romand, R. (1981) Postnatal development of absolute auditory thresholds in kittens. *J. Comp. Physiol. Psychol.* 95, 304-311.

Table M13-0. Audiograms during the first 30 days of postnatal development of *Felis catus* (cat) (Ehret and Romand, 1981).

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
200	107	80	60	51	46	47
300	110					
400	108		53			
500	104	83	50	42	38	37
800	104		49			
1000	104.5	76	47	38	35	34
2000	110	68	51	36	27	26
3000	115					
4000	108	64	40	36	23	22
6000	109	75				
8000		81	50	43	30	31
10000			61		36	36
12000			65	53		
15000			75	61	50	49
20000				71	58	58
25000				76		
30000					68	60
40000					72	62

Notes:

For ages younger than 12 days postnatal, thresholds were determined by observing unconditioned movements of the pinnae and/or facial muscles in response to tone bursts. Animals were restrained with the head free to move, and the responses observed under an operation microscope. Sounds were presented when the animal observed was motionless and not vocalizing. A tone burst was presented once per minute. False alarm rates were measured. A variation of the method of limits was used.

For animals 12 days old or older, movements of the eyelids and pinnae were classically conditioned using shock. Sounds were presented when the animal observed was motionless and not vocalizing. The responses of an animal to three tone presentations at a given frequency and level were counted as "positive" if at least 2 responses were positive and no more than one false alarm occurred during the test interval. A variation of the method of limits was used.

22 kittens were tested from four litters.

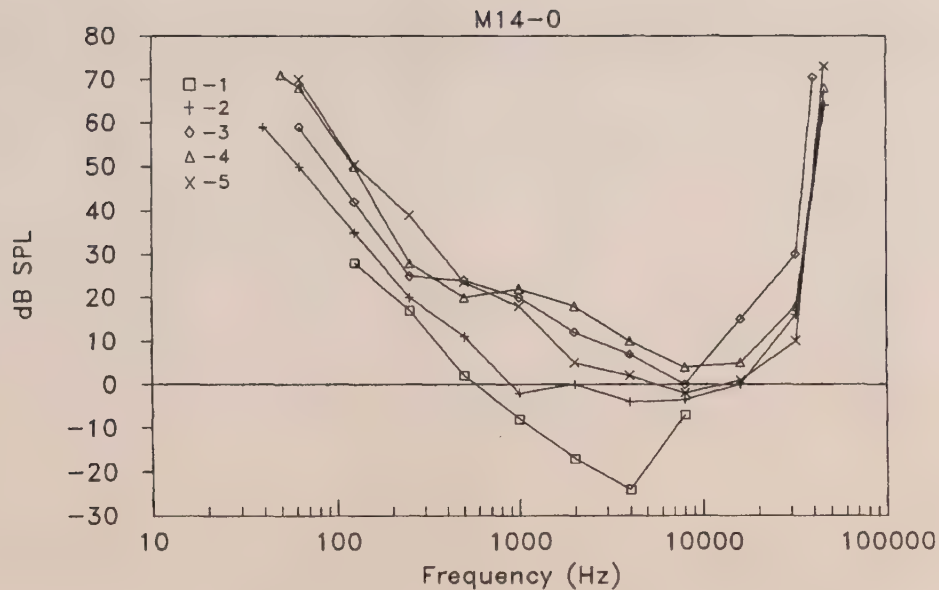


Fig. M14-0. Audiograms for *Canis canis* (dog).

- 1- Dog, Lipman and Grassi (1942)
- 2- Poodle, Heffner (1983)
- 3- Dachshund, Heffner (1983)
- 4- Saint Bernard, Heffner (1983)
- 5- Chihuahua, Heffner (1983)

References:

- Heffner, H.E. (1983) Hearing in large and small dogs: Absolute thresholds and size of the tympanic membrane. *Behav. Neurosci.* 97, 310-318.
- Lipman, E.A. and Grassi, J.R. (1942) Comparative auditory sensitivity of man and dog. *Amer. J. Psychol.* 55, 84-89.

Table M14-0. Audiograms for *Canis canis* (dog).

Frequency (Hz)	dB SPL				
	1	2	3	4	5
40		59			
50				71	
62.5		50	59	68	70
125	28	35	42	50	50.5
250	17	20	25	28	39
500	2	11	24	20	23.5
1000	-8	-2	20	22	18
2000	-17	0	12	18	5
4000	-24	-4	7	10	2
8000	-7	-3.5	0	4	-2
16000		0	15	5	1
32000		16	30	18	10
40000			70.5		
46000		64		68	73

Notes:

1- Conditioned response as described in Culler, Finch, Girden, and Brogden (1935) using the descending method of limits. Data are averages for 11 dogs.

Eighteen humans were also tested similarly in the same apparatus, and the data were presented as the dog thresholds relative to the human thresholds. The data were plotted here in dB SPL by assuming that the humans tested had thresholds equal to those of Sivian and White (1933). The differences between human and dog thresholds given in the paper were plotted here relative to Sivian and White's thresholds.

2-5- Operant conditioning for a food reward using the method of constant stimuli. Water-deprived animals were trained to lick an "observing" spout for water, and then to switch to licking another of two spouts to obtain water. Following a one-second "hold" on the observing spout, a switch to the left spout during tone presentation was reinforced, and a switch to the right spout was reinforced when no tone was presented. One of each of the four types of dogs were tested.

Signals were tones with rise/fall times at least 25 msec or 10 cycles of the signal frequency being tested.

The area of the tympanic membranes of 15 dogs was plotted as a function of body weight, yielding a correlation coefficient of $r=0.83$. The smallest dog (chihuahua) had a tympanic membrane area of about 31 mm² and a body weight of about 4 kg. The largest dog had a tympanic membrane area of about 55 mm² and a weight of about 50 kg. There was no systematic relation between high frequency hearing sensitivity and head size, body weight or tympanic membrane area.

Heffner and Heffner (1984b) measured the effects of section of the brachium of the inferior colliculus on the audiogram for dog and found large (20 to 35 dB) losses of sensitivity at the mid frequencies, and small or negligible losses at the very low (below 100 Hz) and the very high (32 kHz and above) frequencies.

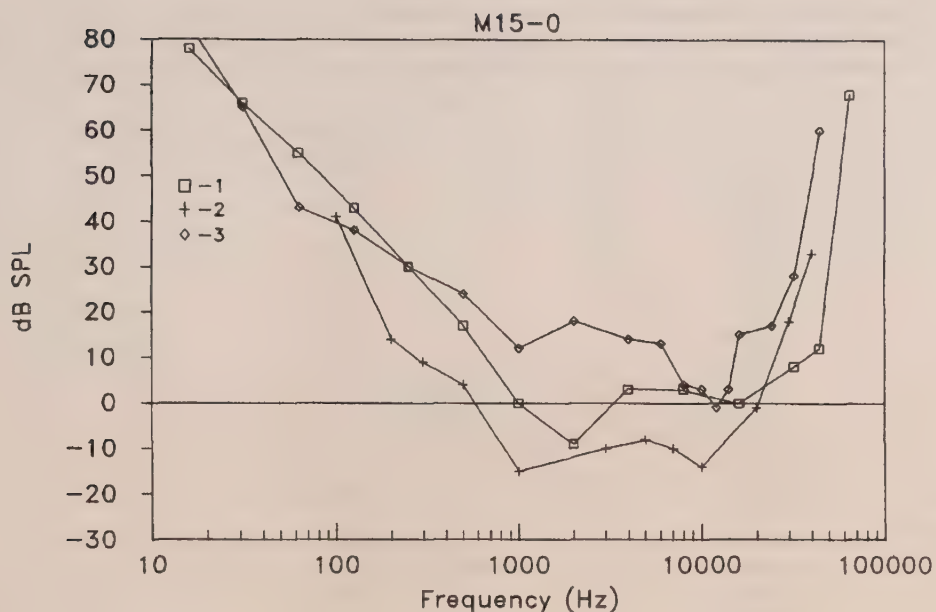


Fig. M15-0. Audiograms for several carnivores.

- 1- *Mustela nivalis* - least weasel (Heffner and Heffner, 1985b)
- 2- *Procyon lotor* - raccoon (Wollack, 1965)
- 3- *Mustela putorius* - ferret (Kelly, Kavanagh, and Dalton, 1986)

References:

- Heffner, R.S., and Heffner, H.E. (1985b) Hearing in mammals: The least weasel. *J. Mammol.* 66, 745-755.
- Kelly, J.B., Kavanagh, G.L., and Dalton, C.H. (1986) Hearing in the ferret (*Mustela putorius*): thresholds for pure tone detection. *Hear. Res.* 24, 269-275.
- Wollack, C.H. (1965) Auditory thresholds in the raccoon (*Procyon lotor*). *J. Aud. Res.* 5, 139-144.

Table M15-0. Audiograms for several carnivores.

Frequency (Hz)	dB SPL		
	1	2	3
16	78		83
31	66		65
62.5	55		43
100		41	
125	43		38
200		14	
250	30		30
300		9	
500	17	4	24
1000	0	-15	12
2000	-9		18
3000		-10	
4000	3		14
5000		-8	
6000			13
7000		-10	
8000	3		4
10000		-14	3
12000			-1
14000			3
16000	0		15
20000		-1	
24000			17
30000		18	
32000	8		28
40000		33	
44000	12		60
64000	68		

Notes:

1- Instrumental shock-avoidance conditioning using the method of constant stimuli. Water-deprived animals were trained to maintain continuous contact with a water spout in order to receive water. By breaking contact with the spout during tone presentation, the animal avoided shock and signalled that it had detected the tone.

This species is the smallest carnivore, and its audiogram is characteristic for carnivores. However, in the absence of middle ear specializations for low frequency hearing, its relatively good sensitivity at low frequencies is unusual among small mammals. Signals were 400 msec tone bursts at 2/sec. Rise/fall times ranged from 10 msec (500 Hz and above) to 150 msec (below 500 Hz). Data averaged over two animals.

2- Operant conditioning for a food reward using a modified method of limits. Animals were trained to wait near a loudspeaker at one end of a cage. Upon sound presentation, the animal was rewarded a grape for crossing the cage and touching the feeder. Signals had 5 msec rise/fall times. Data averaged over two animals.

3- Operant conditioning for a water reward using the descending method of limits. Animals were trained to initiate a trial by nosing a water spout. Following the presentation of a tone, the animals nosed a spout to the right for a reward. If a tone was not presented, the animals nosed a spout on the left for a reward. Signals were 540 msec bursts with 40 msec rise/fall times. Data are means over two animals. The peak in the region of 10 kHz was more pronounced in the data for individuals since it occurred at about 8000 Hz in one animal, and about 12000 Hz in the other.

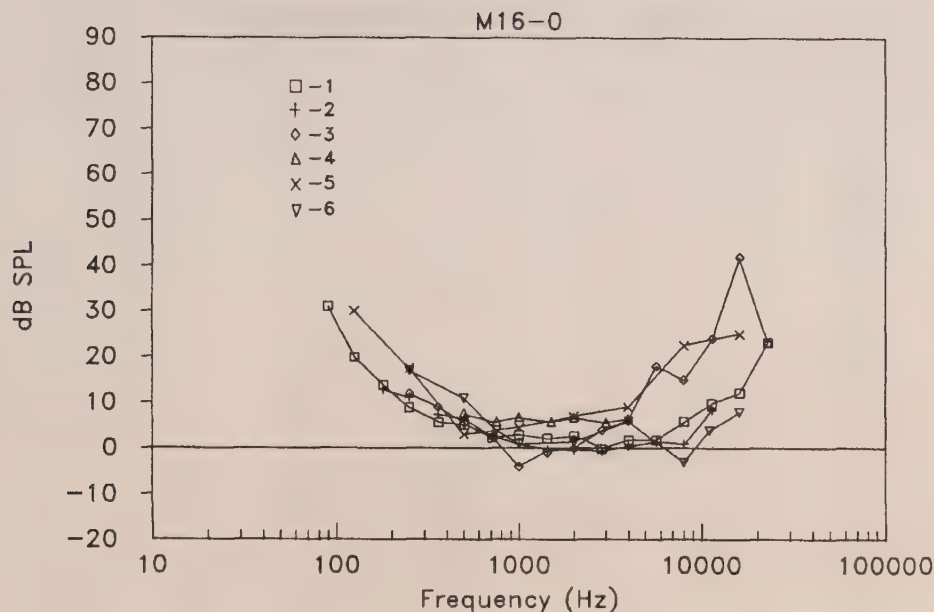


Fig. M16-0. Audiograms for *Chinchilla laniger* (chinchilla).

- 1- Miller (1970)
- 2- Saunders, Mills, and Miller (1977)
- 3- Clark, Clark, Moody, and Stebbins (1974)
- 4- Davis and Ferraro (1984)
- 5- Ades, Trahiotis, Kokko-Cunningham, and Averbuch (1974)
- 6- Salvi, Hamernik, and Henderson (1983)

References:

- Ades, H.W., Trahiotis, C., Kokko-Cunningham, A., and Averbuch, A. (1974) Comparison of hearing thresholds and morphological changes in the chinchilla after exposure to 4 kHz tones. *Acta Otolaryngol.* 78, 192-206.
- Clark, W.W., Clark, C.S., Moody, D.B., and Stebbins, W.C. (1974) Noise-induced hearing loss in the chinchilla, as determined by a positive-reinforcement technique. *J. Acoust. Soc. Amer.* 56, 1202-1209.
- Davis, R. and Ferraro, J. (1984) Comparison between AER and behavioral thresholds in normally and abnormally hearing chinchillas. *Ear and Hearing*, 1984, 5, 153-159.
- Miller, J.D. Audibility curve of the chinchilla *J. Acoust. Soc. Amer.* 1970, 48, 513-523.
- Saunders, J.C., Mills, J.H., and Miller, J.D. (1977) Threshold shift in the chinchilla from daily exposure to noise for six hours. *J. Acoust. Soc. Amer.* 61, 558-570.
- Salvi, R.J., Hamernik, R.P., and Henderson, D. (1983) Response patterns of auditory nerve fibers during temporary threshold shift. *Hear. Res.* 10 37-67.

Table M16-0. Audiograms for *Chinchilla laniger* (chinchilla).

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
90	31					
125	19.9				30	
180	13.9	12.8				
250	8.8	11.1	12		17.5	17
360	5.6	7.4	9			
500	5.1	6.4	5.5	7.7	3	11
715	2.3	2.9	2.5			
750				5.8		4
1000	3	1	-4	6.8	4.5	1
1430	2.2	-0.4	-1			
1500				5.8		
2000	2.7	-0.4	0	6.8	7	1.5
2860	-0.2	-0.7	4			
3000				5.6		
4000	1.9	0.5	6	6.5	9	6
5700	1.9	1.5	18			
8000	5.8	1	15		22.5	-3
11400	9.9	8.4	24			4
16000	12.1		42		25	8
22800	23.1		23			

Notes:

1- Instrumental shock-avoidance in a double grill-box using a modified method of limits. Signals were 750 msec pulses with 50 msec rise/fall times. One ear surgically destroyed. Means: N=34-36. Thresholds were also obtained for binaural chinchillas, and for two "old" chinchillas aged 12 and 14 years. There were no important differences between binaural, monaural, or aged chinchillas.

2- Instrumental shock-avoidance in a double grill-box using a modified method of limits. Signals were three 750 msec pulses with 50 msec rise/fall times. Animals had the left ear surgically destroyed. Data were presented in this paper relative to the mean thresholds from Miller (1970) (shown in function #1, above). The data plotted here are the mean differences over eight animals added to the Miller (1970) thresholds.

3- Operant conditioning for a food reward using a tracking psychophysical procedure. Animals were trained to depress an observing lever and hold it for a variable period (1-6 sec). If the animal released the lever during the 2-sec tone trial, it was reinforced with food. Medians: N=3.

4- Instrumental shock-avoidance in a double-grill box using a modified method of limits. Signals were three, 500 msec tone bursts presented twice per sec. Thresholds were also obtained for 20 msec tone bursts, presented five per sec (data not plotted here). These thresholds averaged 7.16 dB higher than the 500 msec thresholds. This indicates less than perfect (10 dB per decade of duration) temporal summation. Animals with noise damage to the cochlea showed less summation (3.99 dB). Means: N=7.

5- Instrumental shock-avoidance in a double-grill box using a descending method of limits. Signals were 750 msec tone bursts, repeated once per sec with 50 msec rise/fall times. This study also presented thresholds obtained in the presence of relatively flat noise bands (not shown here). Means: N=5.

6- Instrumental shock avoidance in a double grill box using a modified method of limits. One ear surgically destroyed. Signals were 500 msec duration tones with 5 msec rise/fall times. Means: N=6.

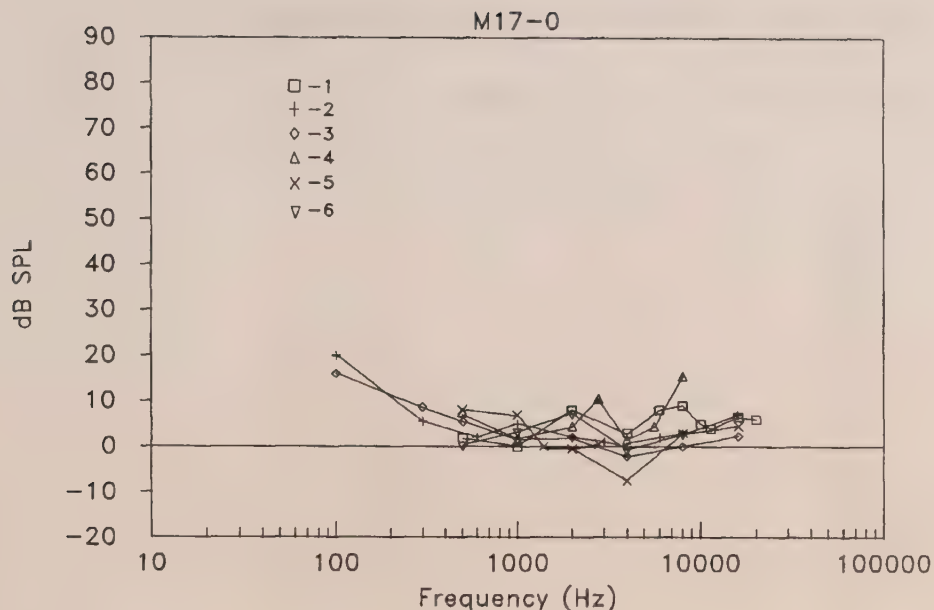


Fig. M17-0. Audiograms for *Chinchilla laniger* (chinchilla).

- 1- Halperin and Dallos (1986)
- 2- Dallos, Harris, Ozdamar, and Ryan (1978)
- 3- McGee, Ryan, and Dallos (1976)
- 4- Henderson, Hamernik, Salvi, and Ahroon (1983)
- 5- Blakeslee, Hynson, Hamernik, and Henderson (1978)
- 6- Henderson, Onishi, Eldredge, and Davis (1969)

References:

- Blakeslee, E.A., Hynson, K., Hamernik, R.P., and Henderson, D. (1978) Asymptotic threshold shift in chinchillas exposed to impulse noise. *J. Acoust. Soc. Amer.* 63, 876-882.
- Dallos, P., Harris, D., Ozdamar, O., and Ryan, A. (1978) Behavioral, compound action potential, and single unit thresholds: relationship in normal and abnormal ears. *J. Acoust. Soc. Amer.* 64, 151-157.
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- Henderson, D., Onishi, S., Eldredge, D., and Davis, H. (1969) A comparison of chinchilla auditory evoked response and behavioral response thresholds. *Percept. Psychophys.* 5, 41-45.
- McGee, T., Ryan, A., and Dallos, P. (1976) Psychophysical tuning curves of chinchillas. *J. Acoust. Soc. Amer.* 60, 1146-1150.

Table M17-0. Audiograms for *Chinchilla laniger* (chinchilla).

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
100		20	16			
300		5.5	8.6			
500	2		5.5	7.5	8	8.5
600		2				
1000	0	5	1.7	1.5	7	3
1400					0	
2000	8	2	2.1	4.5	-0.5	7
2800				10.5	0.5	
3000		1				
4000	3	0	-2.1	1.5	-7.5	-1
5600				4.5		
6000	8	2				
8000	9	3	0	15.5	3	2.5
10000	5					
11400	4					
16000	6.5	7	2.3		4.5	
20000	6					

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli.

Animals were trained to make and hold an "observing response" by pressing a panel. A release during a 3-sec tone presentation resulted in reward. Signals had 10 msec rise/fall times. The probability of a tone presentation following each observing response was 75%. Data are means over three animals.

2- Instrumental shock-avoidance in a double grill-box using a modified method of limits. Signals were 10 msec signals with added 10 msec rise/fall times presented four times/sec for four sec. Data are means over nine animals.

3- Instrumental shock-avoidance in a double grill-box using a modified method of limits. Signals were 3.8 sec tones 10 msec rise/fall times. Data are medians over 3 animals.

4- Instrumental shock-avoidance conditioning using a modified method of limits. Animals were restrained over a shock grid, and trained to lift their feet off the grid in order to avoid shock. Signals were 20 msec tone bursts with 5 msec rise/fall times. Data are medians of three animals.

5- Instrumental shock-avoidance conditioning using a modified method of limits. Animals were restrained over a shock grid, and trained to lift their feet off the grid in order to avoid shock. Signals were eight 500 msec tone bursts with 5 msec rise/fall times repeated once per sec. Data are means over five animals.

6- Instrumental shock-avoidance in a double grill-box using a modified method of limits. Signals were 650 msec tone bursts with 50 msec rise/fall times repeated three times in about 4 sec. Data are means from three animals, each with the left ear destroyed.

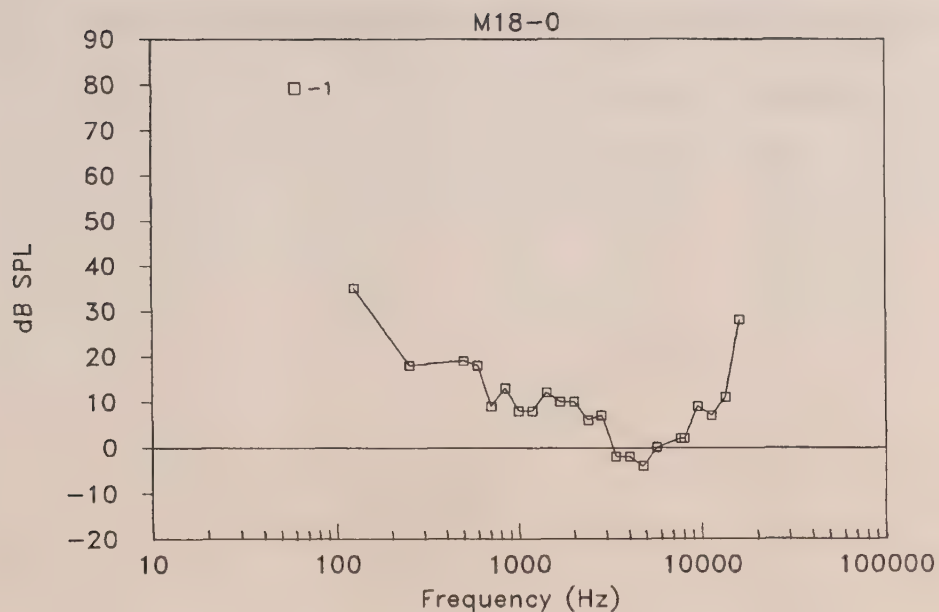


Fig. M18-0. Audiogram for *Chinchilla laniger* (chinchilla) (Clark and Bohne, 1986).

Reference:

Clark, W.W., and Bohne, B.A. (1986) Cochlear damage: Audiometric correlates. In M.J. Collins, T.J. Glatke, and L.A. Harker (eds), *Sensorineural Hearing Loss: Mechanisms, Diagnosis, and Treatment*. University of Iowa Press: Iowa City.

Table M18-0. Audiogram for *Chinchilla laniger* (chinchilla) (Clark and Bohne, 1986).

Frequency (Hz)	dB SPL
125	35
250	18
500	19
595	18
707	9
841	13
1000	8
1189	8
1414	12
1682	10
2000	10
2378	6
2828	7
3364	-2
4000	-2
4757	-4
5657	0
7627	2
8000	2
9513	9
11313	7
13454	11
16000	28

Notes:

Operant conditioning for a food reward using a tracking psychophysical procedure. The animal was trained to depress an observing lever and hold it for a variable period (1-6 sec). If the animal released the lever during the 2-sec tone trial, it was reinforced with food. Left ear destroyed. 10 msec rise/fall times. N=1.

These data are from a book chapter in which other audiometric data (normal and following noise exposure) are reported for the same individual.

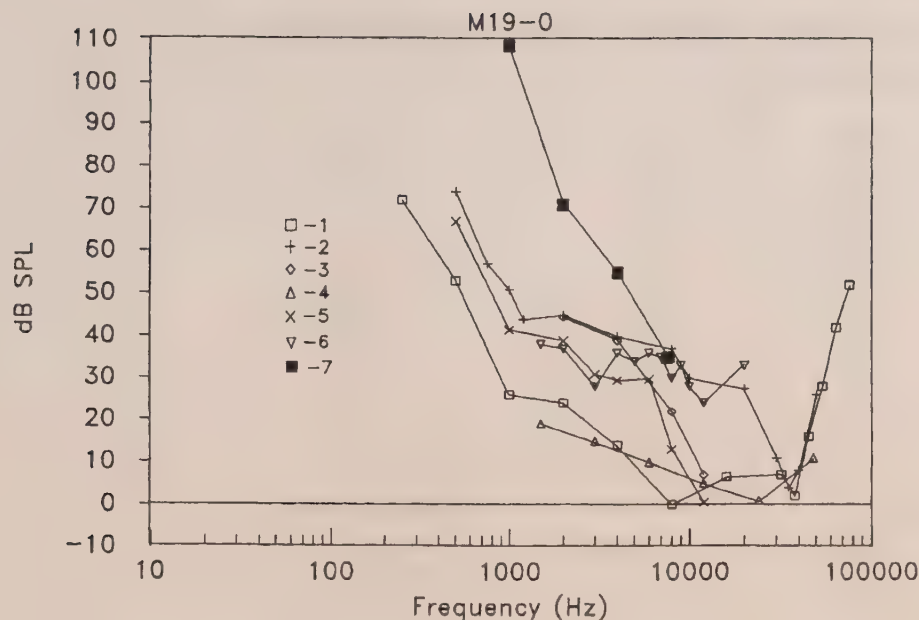


Fig. M19-0. Audiograms for *Rattus norvegicus* (albino rat).

- 1- Kelly and Masterton (1980)
- 2- Gourevitch (1965) and Gourevitch and Hack (1966)
- 3- Jamison (1942)
- 4- Borg (1982)
- 5- Cowles and Pennington (1943)
- 6- Clack and Harris (1963)
- 7- Henry (1938)

References:

- Borg, E. (1982) Auditory thresholds in rats of different age and strain. A behavioral and electrophysiological study. *Hear. Res.* 8, 101-115.
- Cowles, J.T., and Pennington, L.A. (1943) An improved conditioning technique for determining auditory acuity in the rat. *J. Psychol.* 15, 41-47.
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- Henry, F.M. (1938) Audition in the white rat III. Absolute and relative intensity thresholds. *J. Comp. Psychol.* 26, 45-62.
- Gourevitch, G. (1965) Auditory masking in the rat. *J. Acoust. Soc. Amer.* 37, 439-443.
- Gourevitch, G.A., and Hack, M.H. (1966) Audibility in the rat. *J. Comp. Physiol. Psychol.* 62, 289-291.
- Jamison, J.H. (1942) Measurement of auditory intensity thresholds in the rat by conditioning of an autonomic response. *J. Comp. Physiol. Psychol.* 44, 118-125.
- Kelly, J.B., and Masterton, B. (1977) Auditory Sensitivity of the albino rat. *J. Comp. Physiol. Psychol.* 91, 930-936.

Table M19-0. Audiograms for *Rattus norvegicus* (albino rat).

Frequency (Hz)	dB SPL						
	1	2	3	4	5	6	7
250	72						
500	53	74			(512) 64		
750		57					
1000	26	51			(1024) 41.5		110.5
1200		44					
1500				19		38	
2000	24	45	44.5		(2048) 40	37	70.8
3000				15	(2896) 31	28	
4000	14	40	39		(4096) 29	36	55.3
5000						34	
6000				10	(5792) 29	36	
7000						35	
8000	0	37	22		(8192) 15	30	35.6
9000						33	
10000		30				28	
12000			7	5	(11584) 0.5	24	
16000	6.5						
20000		27.5				33	
24000				1			
30000		11					
32000	7						
35000		4					
38000	2						
40000		8					
45000	16						
48000				11			
50000		26					
54000	28						
64000	42						
76000	52						

Notes: See Blackwell and Schlosberg (1943) and Gould and Morgan (1942) for uncalibrated audiograms for the rat.

1- Classically conditioned suppression of an operant response using the method of constant stimuli. Animals licked a spout for water. Tones signalled impending shock suppressing the response. 25-50 msec rise/fall times. Medians: N=3.

2- Operant conditioning with a water reward using a tracking procedure for 500 - 8000 Hz (Gourevitch, 1965; means: N=5) and the method of constant stimuli above 8000 Hz (Gourevitch and Hack, 1966; means: N=3). Animals pressed on one bar in the presence of a tone for water, and pressed another bar for no signal. 250 msec rise/fall times.

3- Classical cardiac conditioning using the method of limits. Means: N=7.

4- Same method as in #1. Animals were three months old. Signals were frequency modulated tones (10 Hz modulation rate with a sweep range increasing from 1 to 10 kHz for center frequencies from 1.5 kHz to 48 kHz). 40 msec rise/fall times. Means: N=10. Audiograms for hypertensive rats and older rats (15 months) and different strains showed no differences. Means: N=3.

5- Classically conditioned vocalization response in restrained animals using the descending method of limits. Parentheses indicate exact frequencies used. Means: N=15.

6- 2-lever method similar to #2 above. Method of constant stimuli. Medians: N=5.

7- Choice in "Y" maze. See Notes for #5, Fig. M37-0. Means: N=22.

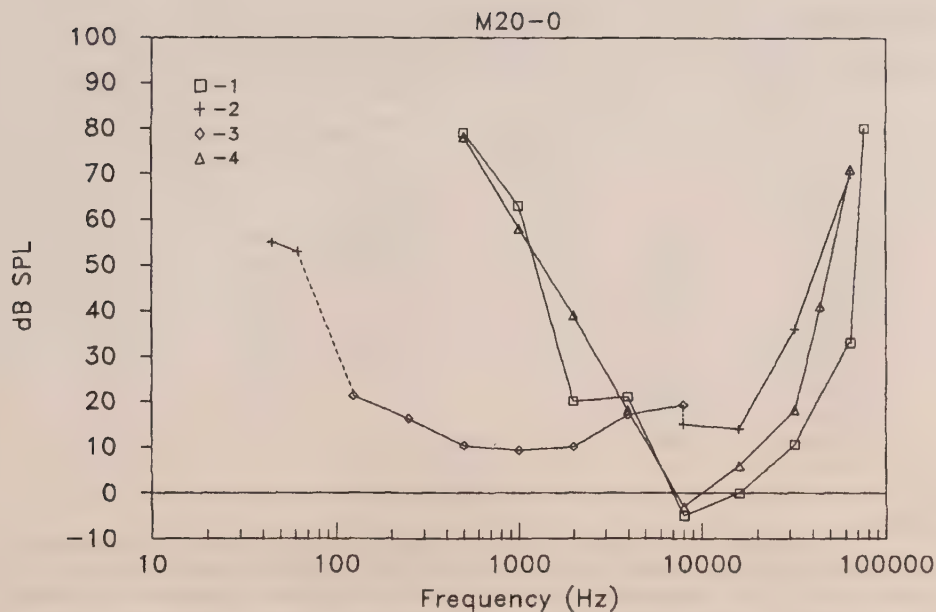


Fig. M20-0. Audiograms for several rats.

- 1- *Sigmodon hispidus* - cotton rat (Heffner and Masterton, 1980)
- 2- *Dipodomys merriami* - kangaroo rat (Heffner and Masterton, 1980)
- 3- *Dipodomys merriami* - kangaroo rat (Webster and Webster, 1972)
- 4- *Neotoma floridiana* - wood rat (Heffner and Heffner, 1985c)

References:

- Heffner, H.E. and Heffner, R.S. (1985c) Hearing in two Cricetid rodents: wood rat (*Neotoma floridiana*) and grasshopper mouse (*Onychomys leucogaster*). J. Comp. Psychol. 99, 275-288.
- Heffner, H.E., and Masterton, B. (1980) Hearing in Glires: Domestic rabbit, cotton rat, house mouse, and kangaroo rat. J. Acoust. Soc. Amer. 68, 1584-1599.
- Webster, D.B., and Webster, M. (1972) Kangaroo rat auditory thresholds before and after middle ear reduction. Brain, Behav. and Evol. 5, 41-53.

Table M20-0. Audiograms for several rats.

Frequency (Hz)	dB SPL			
	1	2	3	4
45		55		
62		53		
125			21.25	
250			16.25	
500	79		10.25	78
1000	63		9.25	58
2000	20		10	39
4000	21		17	18
8000	-5	15	19.25	-3
16000	0	14		6
32000	10.5	36		18
44000				41
64000	33	70		71
76000	80			

Notes:

1- Classically conditioned suppression of licking using a tracking procedure and the method of constant stimuli. Animals were trained to lick a drinking spout for a water reward. Tone presentations signalled impending shock, and suppressed the operant licking behavior. Signals presented through a loudspeaker in front of the animal. Data are means over three animals.

2- Operant conditioning for a food reward using a tracking procedure and the method of constant stimuli. Animals were trained to enter an observing compartment facing a loudspeaker. Animals were then trained to go to a left compartment in the presence of a tone, and to a right compartment if no tone was presented. Data are means for two animals. In the figure above, the dashed lines connect portions of the curve determined by Webster and Webster (1972) and portions determined by Heffner and Masterton (1980).

3- Instrumental shock avoidance using a descending method of limits. Animals were trained to cross to the opposite side of a "tilt box" in the presence of a tone in order to avoid foot shock. Signals were 500 msec shaped tone bursts. Data are means over four animals. In the figure above, the dashed lines connect portions of the curve determined by Webster and Webster (1972) and portions determined by Heffner and Masterton (1980).

4- Instrumental shock avoidance using a tracking procedure and the method of constant stimuli. Animals were trained to maintain contact with a water spout for a water reward, and to break contact in the presence of a tone in order to avoid shock. Signals were 400 msec tone bursts with 10 msec rise/fall times repeated twice per sec. Data are means over two animals.

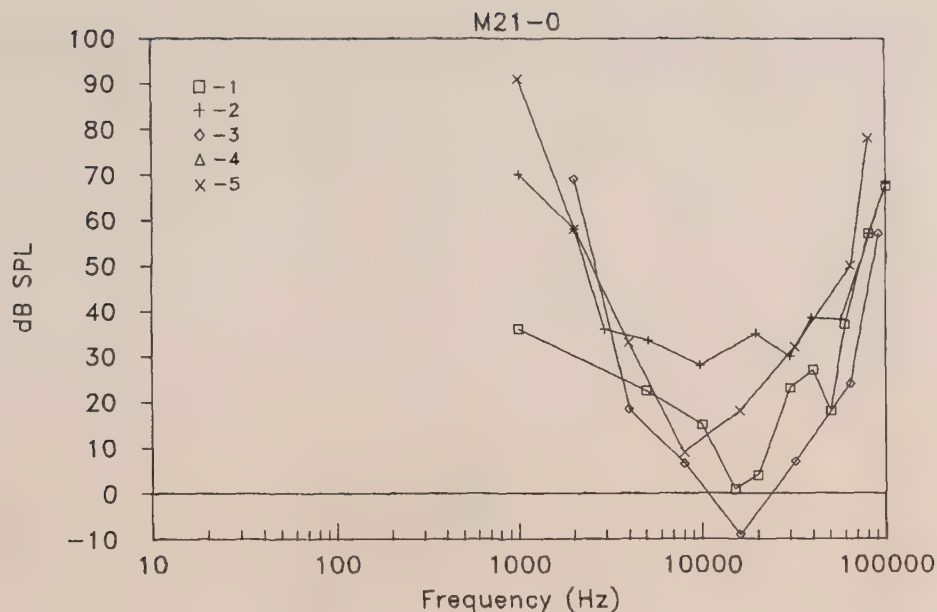


Fig. M21-0. Audiograms for several mice.

- 1- *Mus musculus* - laboratory mouse strain NMRI (Ehret, 1974)
- 2- *Mus musculus* - laboratory mouse strain CBA-J (Birch, Warfield, Ruben, and Mikaelian, 1968)
- 3- *Mus musculus* - feral house mouse (Heffner and Masterton, 1980)
- 4- *Mus musculus* - laboratory mouse strain CBA-J (Berlin, 1963)
- 5- *Onychomys leucogaster* - grasshopper mouse (Heffner and Heffner, 1985c)

References:

- Berlin, C.I. (1963) Hearing in mice via GSR audiometry. *J. Speech Hear. Res.* 6, 359-368.
- Birch, L.M., Warfield, D., Ruben, R.J., and Mikaelian, D.O. (1968) Behavioral measurements of pure tone thresholds in normal CBA-J mice. *J. Aud. Res.* 8, 459-468.
- Ehret, G. (1974) Age-dependent hearing loss in normal hearing mice. *Naturwissenschaften* 11, 506.
- Heffner, H.E. and Heffner, R.S. (1985c) Hearing in two Cricetid rodents: wood rat (*Neotoma floridiana*) and grasshopper mouse (*Onychomys leucogaster*). *J. Comp. Psychol.* 99, 275-288.
- Heffner, H.E., and Masterton, B. (1980) Hearing in Glires: Domestic rabbit, cotton rat, house mouse, and kangaroo rat. *J. Acoust. Soc. Amer.* 68, 1584-1599.

Table M21-0. Audiograms for several mice.

Frequency (Hz)	dB SPL				
	1	2	3	4	5
1000	36	70		91	91
2000		58	69		58
2950		36			
4000			18.5		33
5000	22.5			40	
5100		33.5			
8000			6.5	40	9
9800		28			
10000	15			24	
12000				14	
14000				4	
15000	1			4	
16000			-9		18
18000				9	
19500		35			
20000	4			19	
25000				24	
30000	23	30		34	
32000			7		32
35000				58	
39500		38.5			
40000	27			78	
50000	18				
57000		38.2			
60000	37				
64000			24		50
80000	57				78
81000		57			
91000			57		
99500		68			
100000	67.5				

Notes:

1- Classical conditioning of eyeblink using shock and a modified ascending method of limits. Signals were 100 msec tone bursts with 10 msec rise/fall times. Means: N=13. Similar data in Markl and Ehret (1973) using both the conditioned eyeblink and operant conditioning.

2- Operant conditioning for a water reward using the descending method of limits. Animals moved to one side of a cage near the loudspeaker, and crossed to the other side of the cage and pressed a lever in the presence of a tone for a water reward. Signals were 150 msec tone bursts with 10-20 msec rise/fall times. Means: N=14.

3- Classically conditioned suppression of licking using a tracking procedure and the method of constant stimuli. Animals licked a drinking spout for a water reward. Tone presentations signalled impending shock, and suppressed the operant licking behavior. Signals presented through a loudspeaker in front of the animal. Means: N=3.

4- Classically conditioned galvanic skin response recorded from rear paw pads to shock to front paw pads, using a method of limits. Means: N=50.

5- Instrumental shock avoidance using a tracking procedure and the method of constant stimuli. Animals maintained contact with a water spout for a water reward, and broke contact in the presence of a tone in order to avoid shock. Signals were 400 msec tone bursts with 10 msec rise/fall times repeated twice per sec. Means: N=3.

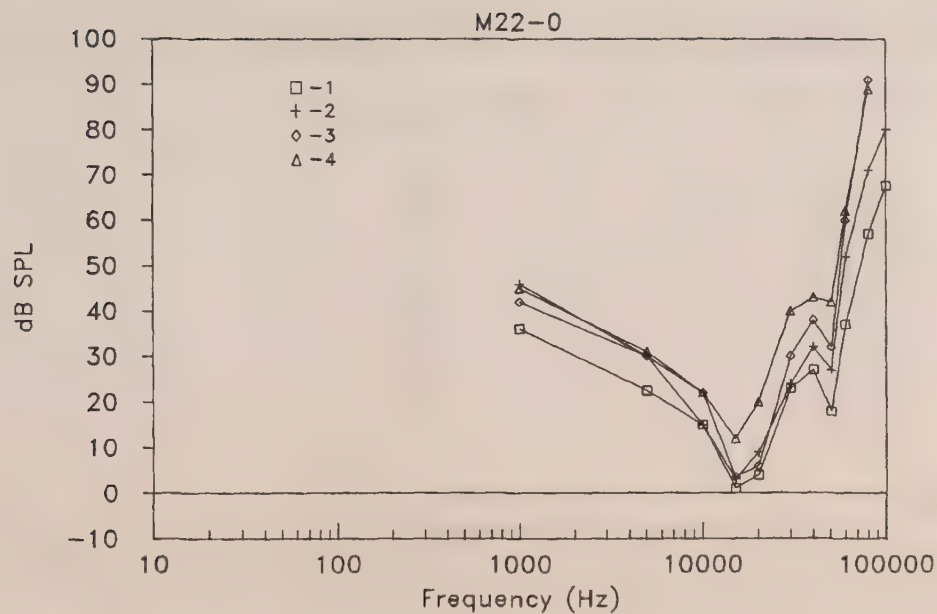


Fig. M22-0. The effect of aging on the audiogram for *Mus musculus* (laboratory mouse) (Ehret, 1974).

- 1- 2-3 months of age (normal control)
- 2- 6-7 months of age
- 3- 12-13 months of age
- 4- 17-18 months of age

Reference:

Ehret, G. (1974) Age-dependent hearing loss in normal hearing mice.
Naturwissenschaften 11, 506.

Table M22-0. The effect of aging on the audiogram for *Mus musculus* (laboratory mouse) (Ehret, 1974).

Frequency (Hz)	dB SPL			
	1	2	3	4
1000	36	46	42	45
5000	22.5	30	30	31
10000	15	15	22	22
15000	1	3	3.5	12
20000	4	9	6	20
30000	23	24	30	40
40000	27	32	38	43
50000	18	27	32	42
60000	37	52	60	62
80000	57	71	91	89
100000	67.5	80		

Notes:

Classical conditioning of eyeblink using shock and a modified ascending method of limits. Signals were 100 msec tone bursts with 10 msec rise/fall times. Data are means over 13 2-3 month old animals, six 6-7 month old animals, six 12-13 month old animals, and six 17-18 month old animals. Similar data were presented for the 2-3 month old animals in Markl and Ehret (1973) using both the conditioned eyeblink and operant conditioning.

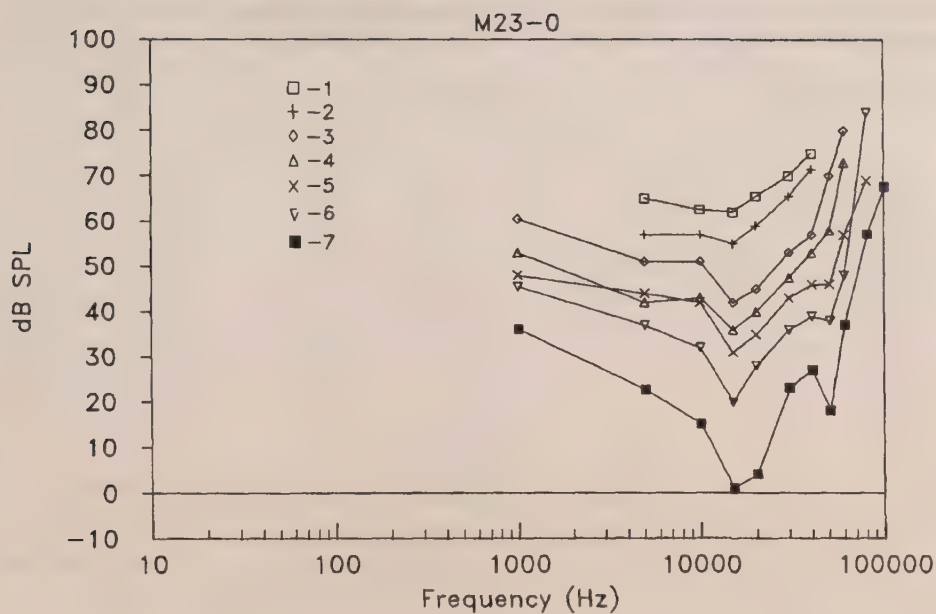


Fig. M23-0. The development of hearing sensitivity in young *Mus musculus* (laboratory mouse) (Ehret, 1976b).

- 1- 11 days old
- 2- 12 days old
- 3- 14 days old
- 4- 15 days old
- 5- 16 days old
- 6- 17-19 days old
- 7- 2-3 months old

Reference:

Ehret, G. (1976b) Development of absolute auditory thresholds in the house mouse (*Mus musculus*). J. Amer. Audiol. Soc. 1, 179-184.

Table M23-0. The development of hearing sensitivity in young *Mus musculus* (laboratory mouse) (Ehret, 1976b).

Frequency (Hz)	dB SPL					
	1	2	3	4	5	6
1000			60.5	53	48	45.5
5000	65	57	51	42	44	37
10000	62.5	57	51	43	42	32
15000	62	55	42	36	31	20
20000	65.5	59	45	40	35	28
30000	70	65.5	53	47.5	43	36
40000	75	71.5	57	53	46	39
50000			70	58	46	38
60000			80	73	57	48
80000					69	84

Notes:

A portion of the most representative data from this study are presented here. Values for intermediate ages (13, 18, 24, 30 days, and seven months) using the pinna reflex are not plotted here but can be found in Ehret (1974) Fig. 1.

1- Unconditioned "stop" reaction upon sound stimulation using a modified ascending method of limits. Freely moving animals were observed to stop moving briefly and to lift the head and "sniff around." Signals were 100 msec tone bursts with 10 msec rise/fall times. Means: N=10.

2-5- Unconditioned pinna movement upon sound stimulation using a modified method of limits. Slowly moving or stopped animals were observed to flick the pinna in response to sound from the side or from behind. This is not the well known Preyer reflex, which is a component of a startle reaction to intense sound. Same signals as in #1. Means: N=10 for each group in #2 to #5.

6- Classical conditioning of eyeblink using shock and a modified ascending method of limits. Same signals as in #1. Means: N=12.

7- The data for 2-3 month old animals using the methods of #6 above, from Table M22-0.

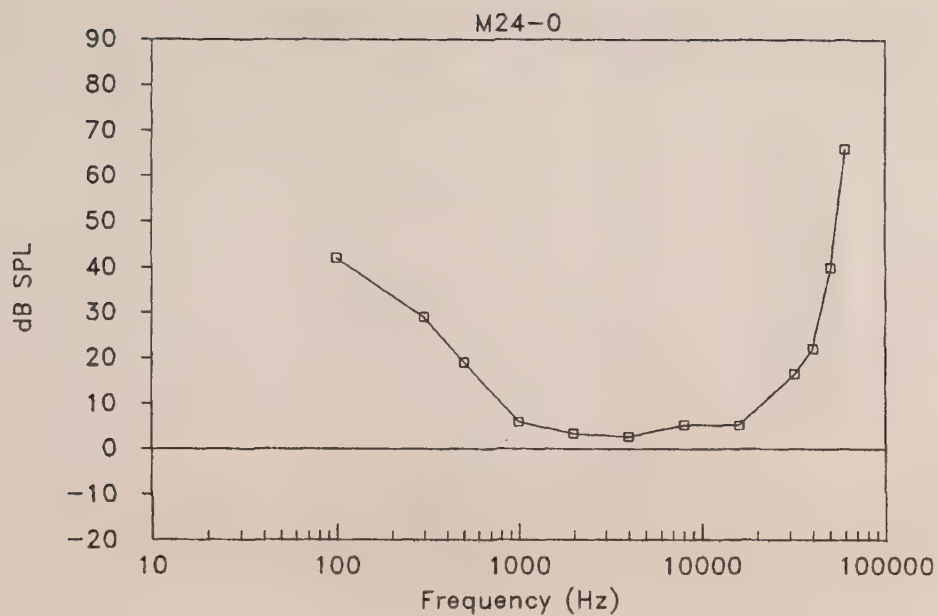


Fig. M24-0. Audiogram for *Meriones unguiculatus* (gerbil) (Ryan, 1976).

Reference:

Ryan, A. (1976) Hearing sensitivity of the mongolian gerbil, *Meriones unguiculatus*.
J. Acoust. Soc. Amer. 59, 1222-1226.

Table M24-0. Audiogram for *Meriones unguiculatus* (gerbil) (Ryan, 1976).

Frequency (Hz)	dB SPL
100	42
300	29
500	19
1000	6
2000	3.4
4000	2.7
8000	5.4
16000	5.3
32000	16.5
40000	22
50000	40
60000	66

Notes:

Instrumental shock avoidance using a method of limits. Animals were trained to cross to the opposite side of a shuttle box in the presence of a tone in order to avoid shock. Signals were 3.8 sec duration tones with 10 msec rise/fall times. Additional thresholds using the method of constant stimuli established psychometric functions for one animal at each frequency (not shown here). Means: N=13.

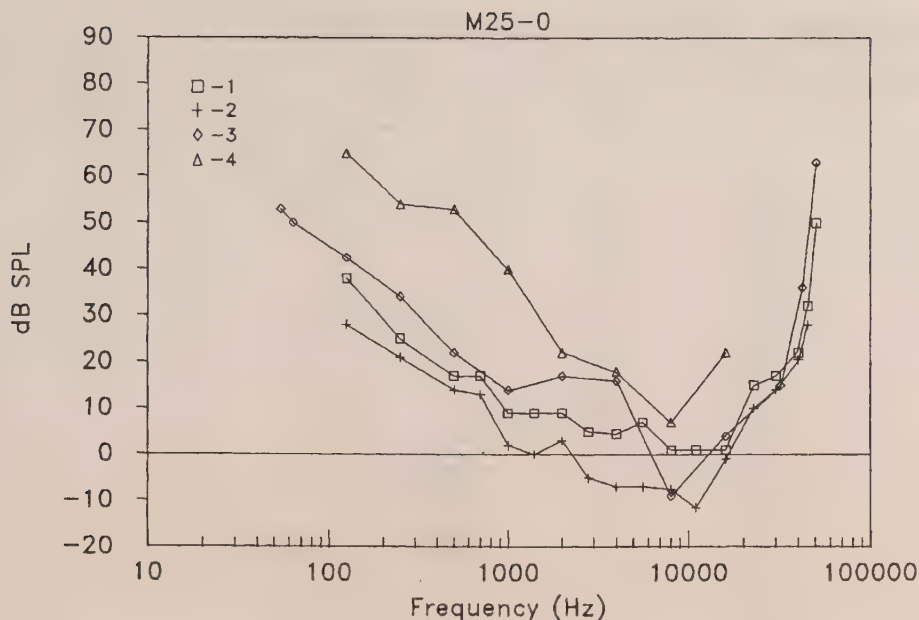


Fig. M25-0. Audiograms for *Cavia procellus* (guinea pig).

- 1- Albino guinea pig (Prosen, Petersen, Moody, and Stebbins, 1978)
- 2- Pigmented guinea pig (Prosen, Petersen, Moody, and Stebbins, 1978)
- 3- Domestic guinea pig (Heffner, Heffner, and Masterton, 1971)
- 4- Pigmented guinea pig (Syka and Popelar, 1980)

References:

- Heffner, R., Heffner, H., and Masterton, R.B. (1971) Behavioral measurement of absolute and frequency-difference thresholds in guinea pig. *J. Acoust. Soc. Amer.* 49, 1888-1895.
- Prosen, C.A., Petersen, M., Moody, D., and Stebbins, W. (1978) Auditory thresholds and kanamycin-induced hearing loss in the guinea pig assessed by a positive reinforcement procedure. *J. Acoust. Soc. Amer.* 63, 559-556.
- Syka, J., and Popelar, J. (1980) Hearing threshold shifts from prolonged exposure to noise in guinea pigs. *Hear. Res.* 3, 205-213.

Table M25-0. Audiograms for *Cavia procellus* (guinea pig).

Frequency (Hz)	dB SPL			
	1	2	3	4
54			53	
63			50	
125	38	28	42.5	65
250	25	21	34	54
500	17	14	22	53
700	17	13		
1000	9	2	14	40
1400	9	0		
2000	9	3	17	22
2800	5	-5		
4000	4.5	-7	16	18
5600	7	-7		
8000	1	-7.5	-9	7
11000	1	-11.5		
16000	1	-1	4	22
22800	15	10		
30000	17	14		
32000			15	
40000	22	20.5		
42000			36	
45000	32	28		
50000	50		63	

Notes:

1-2- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to press a report key with their nose repeatedly. After some variable number of responses, a 2.5 sec tone was presented, and only responses on a second, "report" key were reinforced with food. Signals had 50 msec rise/fall times. Means: N=2 (pigmented) and N=4 (albino) guinea pigs. In this paper, several psychometric functions are presented, and the effects on the audiogram of kanamycin were documented at from 7 to 40 days after the first drug injection. A progressive, high frequency hearing loss was shown.

3- Classically conditioned suppression of an operant response using the method of limits and the method of constant stimuli. Animals were trained to lick a water spout for a water reward on an intermittent reinforcement schedule. Tone presentations signalled impending foot shock and suppressed licking. Signals above 500 Hz had 25 msec rise/fall times. Signals below 500 Hz had longer rise/fall times. Means: N=4. Additional thresholds given for different threshold criteria did not differ in important ways from the thresholds plotted here.

4- Same procedure as for #1-2 above except that water was the reinforcer. Signals were 200 msec tones with 50 msec rise/fall times. Medians: N=3. Data are presented on the time course of the growth and decay of temporary threshold shifts due to noise exposure. Psychometric functions before and after noise exposure are also given.

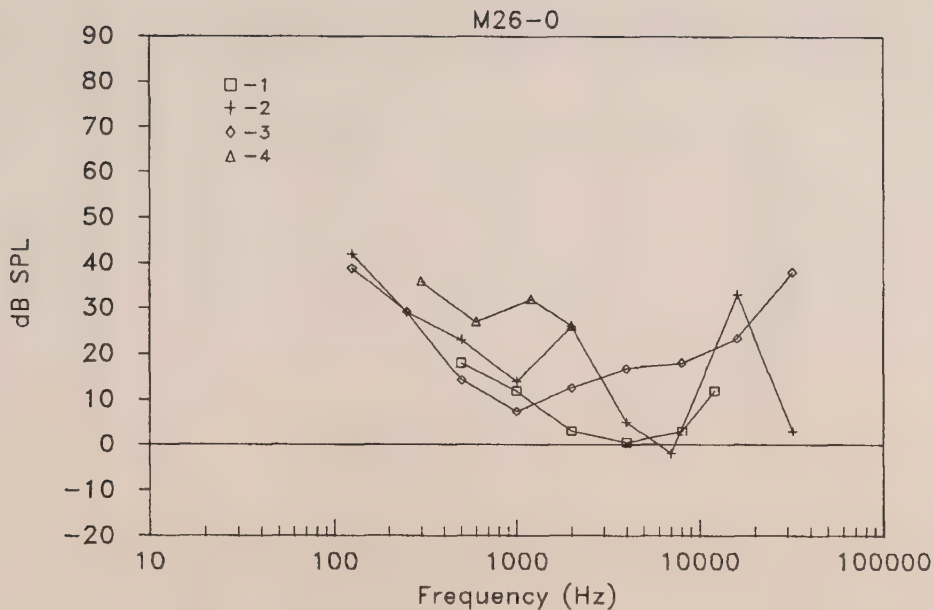


Fig. M26-0. Audiograms for *Cavia procellus* (guinea pig).

- 1- Pigmented guinea pig (Anderson and Wedenberg, 1965)
- 2- Guinea pig (Walloch and Taylor-Spikes, 1976)
- 3- Pigmented guinea pig (Miller and Murray, 1966)
- 4- Guinea pig (Sherrick and Bilger, 1959)

References:

- Anderson, H., and Wedenberg, E. (1965) A new method for hearing tests in the guinea pig. *Acta Oto-Laryngol.* 60, 375-393.
- Miller, J.D., and Murray, F.S. (1966) Guinea pig's immobility response to sound: Threshold and habituation. *J. Comp. Physiol. Psychol.* 61, 227-233.
- Sherrick, C.E. Jr., and Bilger, R.C. (1959) Auditory sensitivity of the guinea pig to low-frequency tones. *Percept. Motor Skills* 9, 339-344.
- Walloch, R.A., and Taylor-Spikes, M. (1976) Auditory thresholds in the guinea pig: A preliminary report on a behavioral technique employing a food reward. *Laryngoscope* 86, 1699-1705.

Table M26-0. Audiograms for *Cavia procellus* (guinea pig).

Frequency (Hz)	dB SPL			
	1	2	3	4
125		42	38.8	
250		29	29.2	
300				36
500	18	23	14.3	
600				27
1000	12	14	7.5	
1200				32
2000	3	26	12.6	26
4000	0.5	5	16.8	
7000		-2		
8000	3		18	
12000	12			
16000		33	23.4	
32000		3	38	

Notes:

1- Classical conditioning of a "shiver" response using the method of limits. Restrained animals were cooled slightly to produce a regular pattern of shivering. Three second tone presentations terminated with a brief shock to the pinnae. A response was defined as a significant modification of the temporal pattern of shivering caused by the tone presentation. Means: N=2. The effects of plugging the ears and intense noise were also investigated along with pinna reflex thresholds.

2- Operant conditioning with a food reward using a tracking procedure. Animals pressed a lever a variable number of times, producing a tone presentation. If the animal stopped pressing within two sec during the tone presentation it was rewarded with food. Trials were presented every 10 to 15 sec. Medians: N=6.

3- Unconditioned "immobility response" using the ascending method of limits. Novel sounds produce a characteristic immobility response, or a brief pause in ongoing activity (chewing lettuce). Signals were 2 sec tone bursts with 150 msec rise/fall times. Medians: N=6.

4- Classical respiratory conditioning using the method of limits. Respiration was measured in animals with one ear plugged. Tones of 4.5 sec duration terminated with shock. The conditioned response was a marked regularity of the respiration record compared with a brief period preceding the tone. Means: N=5.

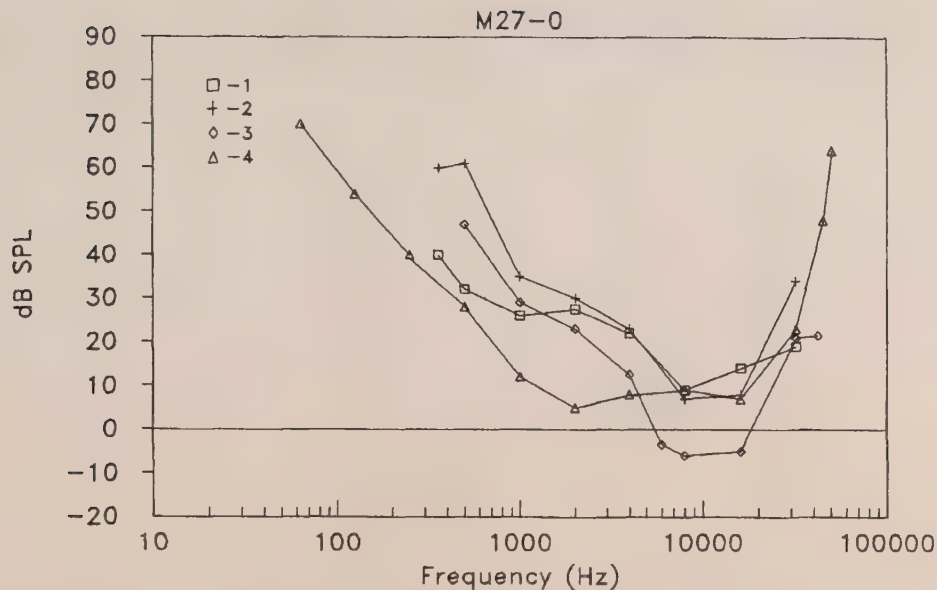


Fig. M27-0. Audiograms for *Oryctolagus cuniculus* (rabbit).

- 1- Pigmented San Juan rabbit (Martin, Lonsbury-Martin, and Kimm, 1980)
- 2- New Zealand white rabbit (Martin, Lonsbury-Martin, and Kimm, 1980)
- 3- Rabbit of the chinchilla strain (Borg and Engstrom, 1983)
- 4- New Zealand white rabbit (Heffner and Masterton, 1980)

References:

- Borg, E., and Engstrom, B. (1983) Hearing thresholds in the rabbit. A behavioral and electrophysiological study. *Acta Oto-Laryngol.* 95, 19-26.
- Heffner, H., and Masterton, R. (1980) Hearing in glires: Domestic rabbit, cotton rat, feral house mouse and kangaroo rat. *J. Acoust. Soc. Amer.* 68, 1584-1599.
- Martin, G., Lonsbury-Martin, B., Kimm, J. (1980) A rabbit preparation for neuro-behavioral research. *Hear. Res.* 2, 65-78.

Table M27-0. Audiograms for *Oryctolagus cuniculus* (rabbit).

Frequency (Hz)	dB SPL			
	1	2	3	4
63				70
125				54
250				40
360	40	60		
500	32	61	47	28
1000	26	35	29	12
2000	27.5	30	23	5
4000	22	23	12.5	8
6000			-3.5	
8000	9	7	-6	9
16000	14	8	-5	7
32000	19	34	21	23
42000			21.5	
45000				48
50000				64

Notes:

1- Classical conditioning of the nictitating membrane using a tracking procedure. Movements of the nictitating membrane were measured during delay conditioning in which the unconditioned stimulus was an electric shock delivered near the eye, and the conditioned stimulus was a 350 msec tone burst presented through earphones. Data are means over two animals.

2- Same as #1, except that thresholds were determined using both a tracking procedure and the method of constant stimuli. Data are means over five animals using both psychophysical procedures.

3- Classically conditioned suppression of licking using a tracking procedure. Animals were trained to lick a drinking spout for a water reward. Tone presentations signalled impending shock, and suppressed the operant licking behavior. Signals presented through earphones. Data are means over three animals.

4- Classically conditioned suppression of licking using a tracking procedure and the method of constant stimuli. Animals were trained to lick a drinking spout for a water reward. Tone presentations signalled impending shock, and suppressed the operant licking behavior. Signals presented through a loudspeaker in front of the animal. Data are means over two animals.

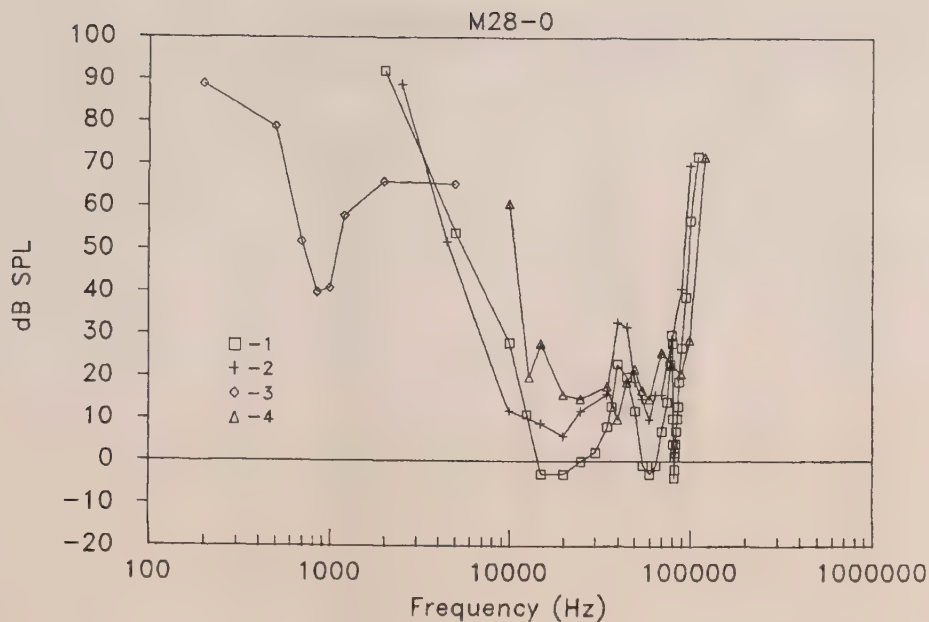


Fig. M28-0. Audiograms for several insectivorous bats.

- 1- *Rhinolophus ferrumequinum* - greater horseshoe bat (Long and Schnitzler, 1975)
- 2- *Eptesicus fuscus* - big brown bat (Dalland, 1965)
- 3- *Eptesicus fuscus* - big brown bat (Poussin and Simmons, 1982)
- 4- *Myotis lucifugus* - little brown bat (Dalland, 1965)

References:

- Dalland, J. (1965) Hearing sensitivity in bats. *Science* 150, 1185-1186.
- Long, G.L., and Schnitzler, H.U. (1975) Behavioural audiograms from the bat *Rhinolophus ferrumequinum*. *J. Comp. Physiol.* 100, 211-219.
- Poussin, C., and Simmons, J.A. (1982) Low-frequency hearing sensitivity in the echolocating bat, *Eptesicus fuscus*. *J. Acoust. Soc. Amer.* 72, 340-342.

Table M28-0. Audiograms for several insectivorous bats.

Frequency (Hz)				Frequency (Hz)			
1	2	3	4	1	2	3	4
200		89		65000	-1	16	
500		79		70000	7	16	26
700		52		80000		29	23
850		40		75000	14		
1000		41		78000	23		
1200		58		79000	30		
2000	92	66		80000	28		
2500		89		80500	10		
4500		52		81000	4		
5000	54	65.5		81500	-4		
10000	28	12	61	82000	-2		
12500	11			82500	1		
13000			20	83000	2		
15000	-3	9	28	83500	4		
20000	-3	6	16	84000	7		
25000	0	12	15	85000	10		
30000	2			86000	13		
35000	8	16	18	87000	19		
37000	13			90000	27	41	21
40000	23	33	10	95000	39		
45000	20	32	19	100000	57	70	29
50000	12	19	22	110000	72		
55000	-1	15	17	120000			72
60000	-3	10	15				

Notes:

1- Classical cardiac conditioning using the staircase psychophysical procedure. Restrained animals received a six sec conditioned stimulus consisting of 30 msec tone pulses repeated 10 per sec with rise fall times from 0.5 to 10 msec. An air puff to the face of electric shock was the unconditioned stimulus. Data are shown for one of three animals. Detailed audiograms for all three animals in the 80 kHz region are shown in Fig. M29-0.

2- Operant conditioning for a food reward using the descending method of limits. Animals made an observing response, and a tone was presented following a variable length of time. Upon tone presentation, the animal was rewarded with a meal worm for leaving the observing position for a feeding area of the cage within 5 sec of tone onset. N=1.

3- Operant conditioning for a food reward using the descending method of limits. Animals on a "Y" platform were rewarded with a meal worm for crawling to the arm of the platform closest to the speaker emitting sound. The two loudspeakers were 3 m from the animal, separated by 40°. Signals were 100 msec tone bursts with 10 msec rise/fall times. Means: N=2.

4- Same methods as #2. N=1.

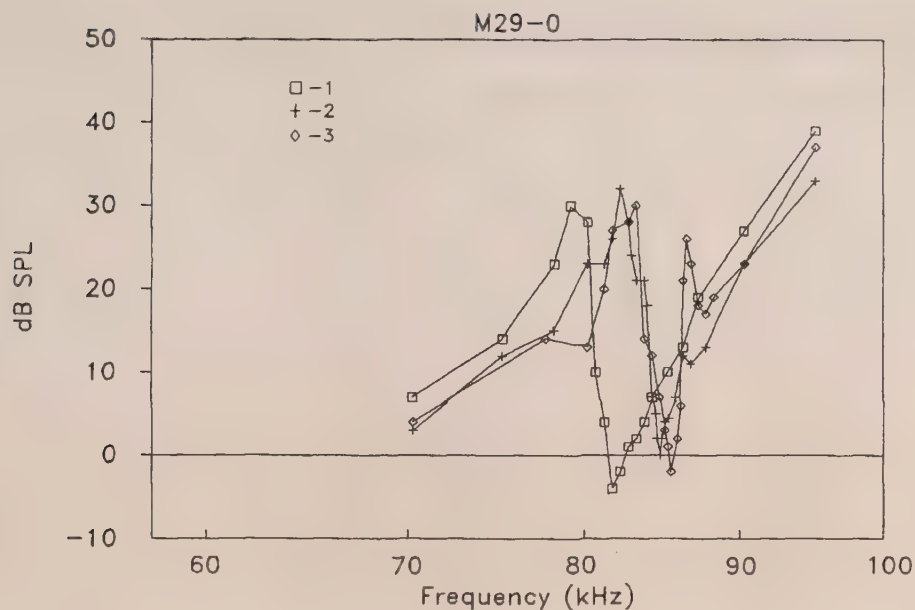


Fig. M29-0. Audiograms for three *Rhinolophus ferrumequinum* (greater horseshoe bat). Detail from Long and Schnitzler (1975).

- 1- Animal L7
- 2- Animal L3
- 3- Animal L6

Reference:

Long, G.L., and Schnitzler, H.U. (1975) Behavioural audiograms from the bat *Rhinolophus ferrumequinum*. J. Comp. Physiol. 100, 211-219.

Table M29-0. Audiograms for three *Rhinolophus ferrumequinum* (greater horseshoe bat). Detail from Long and Schnitzler (1975).

Frequency (Hz)	dB SPL		
	1	2	3
70000	7	3	4
75000	14	12	
77500			14
78000	23	15	
79000	30		
80000	28	23	13
80500	10		
81000	4	23	20
81500	-4	26	27
82000	-2	32	
82500	1	28	28
82700		24	
83000	2	21	30
83500	4	21	14
83700		18	
84000	7	7	12
84200		5	
84300		2	
84500		0	7
84600		2	
84800		4	3
85000	10	4.5	1
85200			-2
85500		7	
85600			2
85800			6
86000	13	12	21
86200			26
86500		11	23
87000	19		18
87500		13	17
88000			19
90000	27	23	23
95000	39	33	37

Notes:

Detail from more complete audiograms for three individuals. The complete audiogram for L7 can be found in Fig. M28-0. The point of maximum sensitivity in the region from 82 to 85 kHz is approximately equal to the frequency of the constant frequency component of that individual's biosonar orientation sound. These data show that the best frequency of the audiogram and the frequency of the orientation sound are highly correlated and a characteristic of individuals.

Classical cardiac conditioning using the staircase psychophysical procedure. Restrained animals received a six sec conditioned stimulus consisting of 30 msec tone pulses repeated 10 per sec with rise fall times from 0.5 to 10 msec. An air puff to the face or electric shock was the unconditioned stimulus.

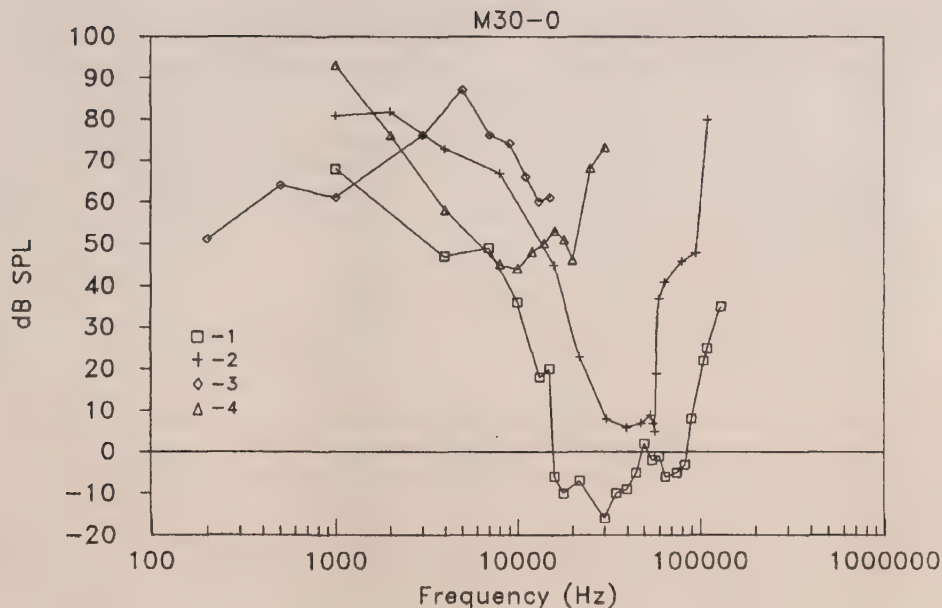


Fig. M30-0. Audiograms for several non-insectivorous bats.

- 1- *Megaderma lyra* - ground gleaning bat (Schmidt, Turke, and Vogler, 1983)
- 2- *Noctilio leporinus* - fish-catching bat (Wenstrup, 1984)
- 3- *Trachops cirrhosus* - frog-eating bat (Ryan, Tuttle, and Barclay, 1983)
- 4- *Rousettus aegyptiacus* - fruit-eating bat (Suthers and Summers, 1980)

References:

- Ryan, M.J., Tuttle, M.D., and Barclay, R.M.R. (1983) Behavioral responses in the frog-eating bat, *Trachops cirrhosus*, to sonic frequencies. *J. Comp. Physiol.* 150, 413-418.
- Schmidt, S., Turke, B., and Vogler, B. (1983) Behavioural audiogram from the bat, *Megaderma lyra* (Geoffroy, 1810; Microchiroptera). *Myotis* 21/22, 62-66.
- Suthers, R.A., and Summers, C.A. (1980) Behavioral audiogram and masked thresholds of the megachiropteran echolocating bat, *Rousettus*. *J. Comp. Physiol.* 136, 227-233.
- Wenstrup, J.J. (1984) Auditory sensitivity in the fish-catching bat, *Noctilio leporinus*. *J. Comp. Physiol.* 155, 91-101.

Table M30-0. Audiograms for several non-insectivorous bats.

Frequency (Hz)	dB SPL				Frequency	dB SPL			
	1	2	3	4		1	2	3	4
					31000		8		
200			51		35000	-10			
500			64		40000	-9	6		
1000	68	81	61	93	45000	-5			
2000		82		76	48000		7		
3000			76		50000	2			
4000	47	73		58	54000				
5000			87		55000	-2			
7000	49		76		56000				
8000		67		45	57000		5		
9000			74		58000		19		
10000	36			44	60000	-1	37		
11000			66		64000		41		
12000				48	65000	-6			
13000			60		75000	-5			
13300	18				80000		46		
14000				50	83000	-3			
15000	20		61		90000	8			
16000	-6	45		53	95000		48		
18000	-10			51	105000	22			
20000				46	110000	25	80		
22000	-7	23			130000	35			
25000				68					
30000	-16			73					

Notes:

1- This audiogram was presented by Neuweiler (1984) in a review paper. This species preys on rodents and other small ground-living animals.

2- Operant conditioning for a food reward using the descending method of limits. Animals were trained to make an observing response facing a loudspeaker, and to go to the right when a tone was presented, and to go left when no tone was presented. Signals were 50 msec tone bursts with 10 msec rise/fall times repeated five times/sec. These data are for one of three animals tested. Details of the audiograms for all three animals appear in Fig. M31-0.

3- Unconditioned orientation response to sound using a type of tracking procedure. Animals hanging from a cage were observed to cock their ears and turn toward a sound source. Signals were 500 msec tone bursts with 50 msec rise/fall times repeated once per 2.3 sec. Means: N=4.

4- Operant conditioning for a food reward using the descending method of limits. Animals were trained to hang from the ceiling of the cage as an observing response, and to wait a variable period for a tone presentation. If the animal left its platform and went to a feeding area within five sec of the tone presentation, it was rewarded with a piece of fruit. Signals were 100 msec tone bursts with 20 msec rise/fall times repeated twice per sec. N=1.

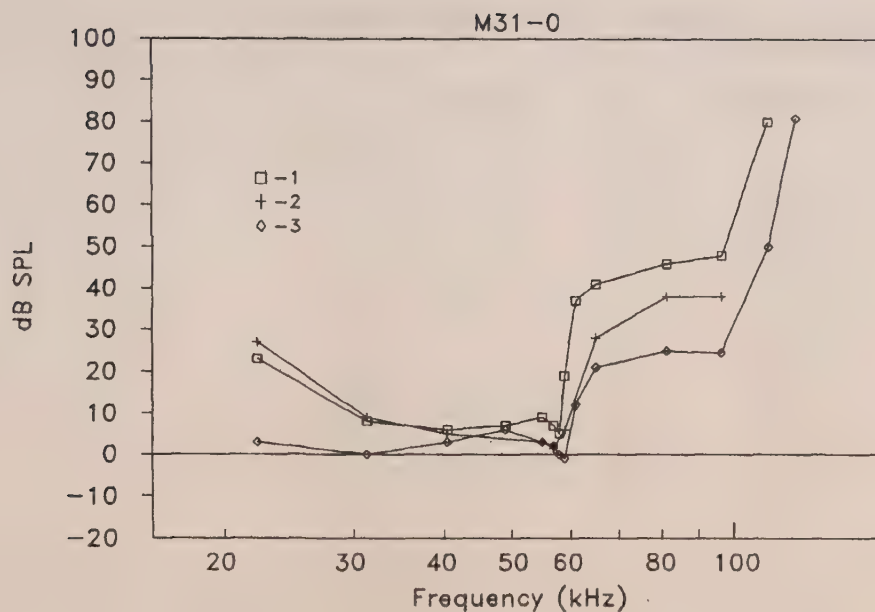


Fig. M31-0. Audiograms for three *Noctilio leporinus* (fish-catching bat). Detail from Wenstrup (1984).

- 1- Animal NL 9
- 2- Animal NL 7
- 3- Animal NL 21

Reference:

Wenstrup, J.J. (1984) Auditory sensitivity in the fish-catching bat, *Noctilio leporinus*. J. Comp. Physiol. 155, 91-101.

Table M31-0. Audiograms for three *Noctilio leporinus* (fish-catching bat). Detail from Wenstrup (1984).

Frequency (Hz)	dB SPL		
	1	2	3
22000	23	27	3
31000	8	9	0
40000	6	5	3
48000	7		6
54000	9	3	3
56000	7	1.5	2
57000	5		0
58000	19	6	-1
60000	37		12
64000	41	28	21
80000	46	38	25
95000	48	38	24.5
110000	80		50
120000			81

Notes:

Detail from more complete audiograms for three individuals. The complete audiogram for NL 9 can be found in Fig. M30-0. The point of maximum sensitivity in the region of 57 kHz is approximately equal to the frequency of the constant frequency component of that individual's biosonar orientation sound. There seem to be small differences among individuals in the peak frequency in the audiogram and the frequency of the orientation sound.

Operant conditioning for a food reward using the descending method of limits. Animals were trained to make an observing response facing a loudspeaker, and to go to the right when a tone was presented, and to go left when no tone was presented. Signals were 50 msec tone bursts with 10 msec rise/fall times repeated five times/sec.

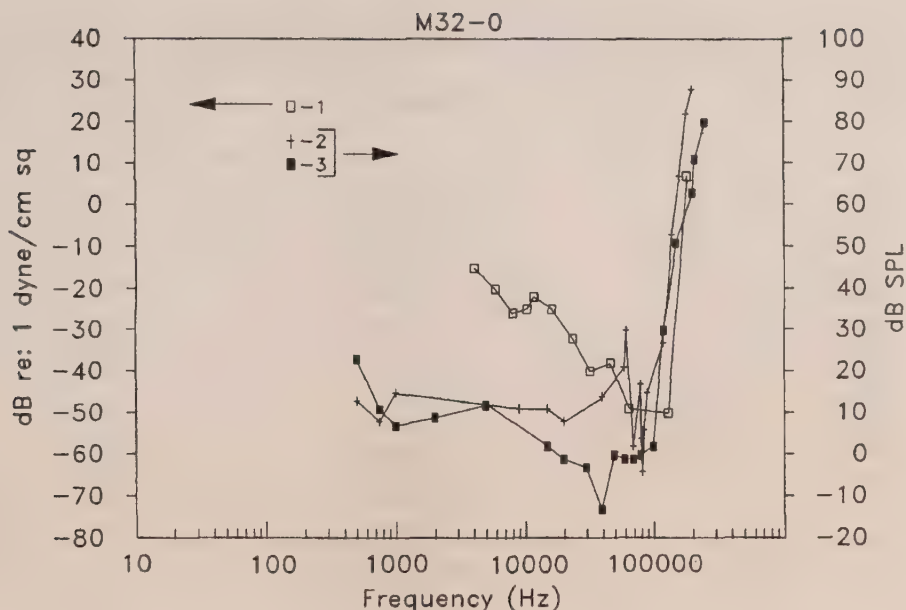


Fig. M32-0. Audiograms for several echolocating mammals derived from a review of the Russian literature (Ayrapet'yants, and Konstantinov, 1974)

- 1- *Phocaena phocaena* - "common" dolphin (harbor porpoise) (Supin and Sukhoruchenko, 1970)
- 2- *Rhinolophus ferrumequinum* - greater horseshoe bat (Ayrapet'yants, and Konstantinov, 1974)
- 3- *Myotis oxygnathus* - a large, little brown bat (Ayrapet'yants, and Konstantinov, 1974)

References:

- Ayrapet'yants, E. Sh., and Konstantinov, A.I. (1974) Echolocation in nature (two volumes). An English translation of the National Technical Information Service, Springfield, VA, JPRS 63328-1 and -2.
- Supin, A. Ya., and Sukhoruchenko, M.N. (1970) Determination of the auditory thresholds of dolphins by the conditioned galvanic skin response (*Phocaena phocaena*). Tr. Akust. Inst. No. 12, 194-199. (In Russian).

Table M32-0. Audiograms for several echolocating mammals derived from a review of the Russian literature (Ayrapet'yants, and Konstantinov, 1974)

Frequency (Hz)	dB re: 1 dyne cm ⁻²	Frequency (Hz)	dB SPL	
	1		2	3
4000	-15	500	23	13
5800	-20	750	11	8
8000	-26	1000	7	15
10300	-25	2000	9	
11600	-22	5000	12	
16000	-25	9000		11
23400	-32	15000	2	11
32000	-40	20000	-1	8
46200	-38	30000	-3	
64000	-49	40000	-13	14
128000	-50	50000	0	
180000	7	60000	-1	21
		62000		30
		70000	-1	2
		80000	0	17
		81000		4
		83000		-4
		85000		6
		90000		15
		100000	2	
		120000	30	27
		140000		53
		150000	51	
		160000		67
		180000		82
		200000	63	88
		210000	71	
		250000	80	

Notes:

1- Classically conditioned galvanic skin reflex using a descending method of limits. These data were derived from a review of the Russian literature by Ayrapet'yants and Konstantinov (1974), translated into English. Details of the methods were not given. The interested reader is referred to the original paper (in Russian).

The review paper also presents audiograms determined with the sound projector at three azimuths relative to the animal (0°, 90°, and 135°), producing an increase in threshold of 8 and 16 dB, respectively, with reference to the 0° azimuth case at about 90 kHz. This difference declined with frequency and disappeared at about 30 kHz. The authors state that this supports the notion that the external ear region is an important pathway of sound to the ear at 30 kHz and below, but that the mandible is an important pathway in the 90 kHz region.

2-3- These data are reported in the review as if for the first time. Operant conditioning for a food reward using a method of descending limits. Animals were trained to move toward (left or right) the source of the signal (five sec pure tone bursts). N=9 *Myotis*, N=6 *Rhinolophus*.

Note that the two bat species tested have significantly lower thresholds at the low frequencies compared with data for the same species or genus from other laboratories (Fig. M28-0).

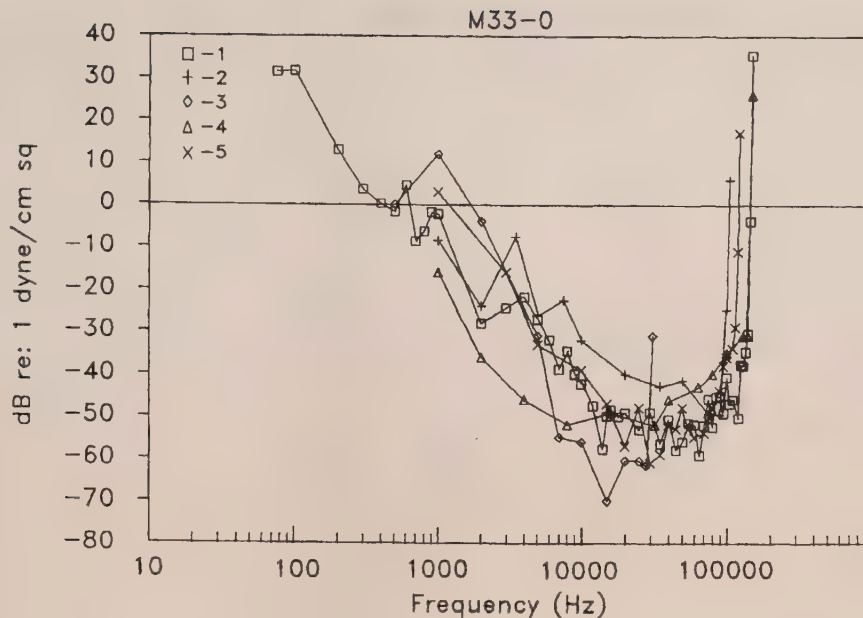


Fig. M33-0. Audiograms for several cetaceans.

- 1- *Tursiops truncatus* - bottlenose porpoise (Johnson, 1967)
- 2- *Inia geoffrensis* - Amazon river dolphin (Jacobs and Hall, 1971)
- 3- *Orcinus orca* - killer whale (Hall and Johnson, 1971)
- 4- *Phocoena phocoena* - harbour porpoise (Andersen, 1970)
- 5- *Delphinapterus leucas* - beluga whale (White, Norris, Ljungblad, Baron, and di Sciara, 1977)

References:

- Andersen, S. (1971) Auditory sensitivity of the harbor porpoise *Phocoena phocoena*. In G. Pilleri (ed), Investigations on Cetacea, Vol. III. University of Berne: Berne, pp. 255-259.
- Hall, J.D., and Johnson, C.S. (1972) Auditory thresholds of a killer whale *Orcinus orca* Linnaeus. J. Acoust. Soc. Amer. 51; 515-517.
- Jacobs, D.W., and Hall, J.D. (1972) Auditory thresholds of a freshwater dolphin, *Inia geoffrensis* Blainville. J. Acoust. Soc. Amer. 51, 530-533.
- Johnson, C.S. (1967) Sound detection thresholds in marine mammals. In W. N. Tavolga (ed), Marine Bio-Acoustics II. Pergamon: Oxford. pp. 247-260.
- White, M.J., Norris, J. Ljungblad, D., Baron, K., and Di Sciara, G. (1978) Auditory thresholds of two beluga whales. Hubbs/Sea World Research Inst. Tech. Rept. No. 78-109.

Table M33-0. Audiograms for several cetaceans.

Frequency		dB re: 1 dyne cm ⁻²					Frequency		dB re: 1 dyne cm ⁻²				
(Hz)		1	2	3	4	5	(Hz)		1	2	3	4	5
75	31.5						25000	-53.2			-60.5		-49
100	31.7						28000				-61.5		
200	12.9						30000	-49					-61
300	3.6						31000				-31		
400	0.2						32000					-52	
500	-1.7			0			35000	-56.4	-42.8				-59
600	4.6						40000	-50.7				-46	-52
700	-8.7						45000	-58					
800	-6.3						50000	-56	-41.5				-48
900	-1.8						55000	-51.6					-53
1000	-2.2	-8.5	12	-16		3	60000	-52					-55
2000	-28.1	-2	-4	-36			64000					-43	
3000	-24.3					-16	65000	-52.9					
3500		-7.5					70000	-52.1					-54
4000	-21.8				-46		75000	-45.9	-49.4				-51
5000	-27.1	-26	-31		-33		80000	-52.6				-40	-48
							85000	-45.4					
6000	-32						90000	-45.1	-49.5				-44
7000	-38.8			-55			95000	-49.2					-38
7500		-22.5					100000	-40.7	-24.7			-35	-36
8000	-34.5				-52		105000	-47	6				
9000	-40						110000	-46					-34
10000	-42.2	-32	-56		-39		115000						-29
10500							120000	-50.4					-11
12000	-47.5						123000	-37.7					+17
14000	-57.7						130000	-38.1				-31	
15000	-49.9		-70		-47		135000	-34.8					
16000	-48.4				-49		140000	-30.5				-31	
18000	-50.1						145000	-3.9					
20000	-49.1	-40	-60.0		-57		150000	35.5				26	

Notes:

1- Operant conditioning for a food reward using a tracking procedure. Animals were trained to swim into a small area and to push a lever to begin a trial. This produced a tone stimulus with a certain probability, and the animals was rewarded for leaving the area and pushing a second lever in the presence of a tone. N=1.

2- Operant conditioning for a food reward using a tracking procedure. Animals were trained to station at a particular point, and in the presence of a tone to leave the station and swim to the other side of a tank, push a lever and receive a reward. N=1.

3- Operant conditioning for a food reward using a tracking procedure. Animals were trained to station, and in the presence of a tone to leave the station and swim to the other side of a tank, push a lever and receive a reward. N=1.

4- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to station at a particular point, and in the presence of a tone to leave the station and swim to the other side of a tank, push a lever and receive a reward. Signals were 1.5 sec tones (rise/fall times of 50 and 100 msec). N=1.

5- Operant conditioning for a food reward. Animals trained to release a mouth grip in the presence of a tone for a reward. Means: N=2. Female more sensitive than male. This reference also plots audiograms for *Tursiops truncatus* (Morozov, et al, 1971) and *Phocoena phocoena* (Sukhoruchenko, 1973). These papers (in Russian) report thresholds below about 80 kHz to be 10 to 20 dB above those shown here for these species.

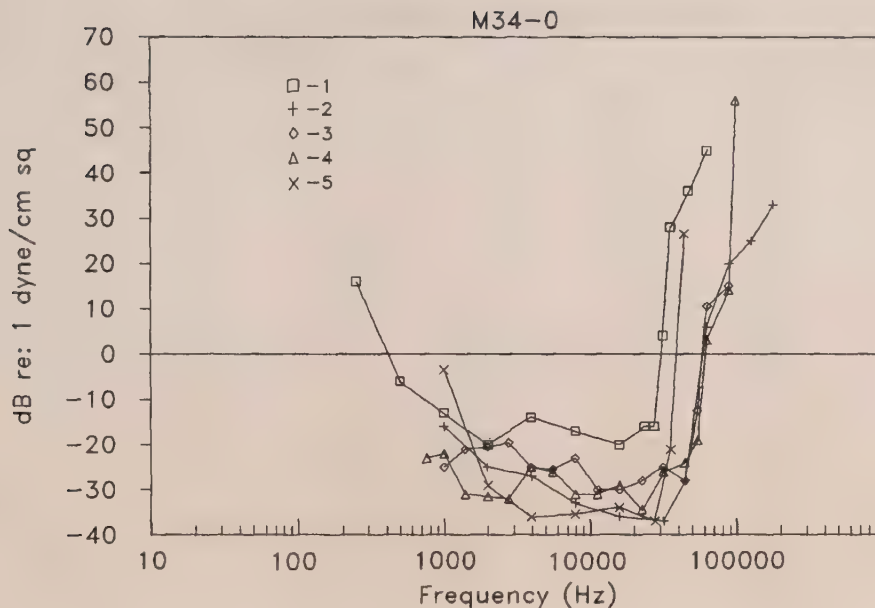


Fig. M34-0. Underwater audiograms for several pinnipeds.

- 1- *Zalophus californianus* - California sea lion (Schusterman, Balliet, and Nixon, 1972)
- 2- *Phoca vitulina vitulina* - harbour seal (Mohl, 1968)
- 3- *Pusa hispida* - ringed seal (Terhune and Ronald, 1975a)
- 4- *Pagophilus groenlandicus* - harp seal (Terhune and Ronald, 1972)
- 5- *Callorhinus ursinus* - Northern fur seal (Schusterman and Moore, 1978a)

References:

- Mohl, B. (1968) Auditory sensitivity of the common seal in air and water. *J. Aud. Res.* 8, 27-38.
- Schusterman, R.J., Balliet, R.F., and Nixon, J. (1972) Underwater audiogram of the California sea lion by the conditioned vocalization technique. *J. Exp. Anal. Behav.* 17, 339-350.
- Schusterman, R.J., and Moore, P.W.B. (1978a) Underwater audiogram of the northern fur seal (*Callorhinus ursinus*). *J. Acoust. Soc. Amer.* 64, S87 (abstract). Cited in Watkins, W.A., and Wartzok, D. (1985) Sensory biophysics of marine mammals. *Marine Mammal Science* 1, 219-260.
- Terhune, J.M., and Ronald, K. (1972) The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777), III. The Underwater audiogram. *Can. J. Zool.* 50, 565-569.
- Terhune, J.M., and Ronald, K. (1975a) Underwater hearing sensitivity of two ringed seals (*Pusa hispida*). *Can. J. Zool.* 50, 565-569.

Table M34-0. Underwater audiograms for several pinnipeds.

Frequency (Hz)	dB re: 1 dyne cm ⁻²				
	1	2	3	4	5
250	16				
500	-6				
760				-23	
1000	-13	-16	-25	-22	-3.5
1400			-21	-31	
2000	-20	-25	-20.5	-31.5	-29
2800			-19.5	-32	
4000	-14	-27	-25	-25	-36
5600			-25.5	-26	
8000	-17	-33	-23	-31	-35.5
11300			-30	-31	
16000	-20	-36	-30	-29	-34
22900			-28	-34.5	
24000	-16				
28000	-16				-37
32000	4	-37	-25	-26	
36000	28				-21
44900			-28	-24	26.5
45000		-28			
48000	36				
55000			-12.5	-19	
64000	45	6	10.5	3	
90000		20	15	14	
100000				56	
128000		25			
180000		33			

Notes:

1- Operant conditioning of a vocal response for food reward using a modified method of limits. Animals were trained to "station" at a fixed position, and to emit "click" vocalizations in the presence of a tone signal in order to receive a food reward. Tone signals had 100 msec rise/fall times. This study presents several psychometric functions. N=1.

2- Operant conditioning with a food reward using the method of constant stimuli. Animals were trained to make a response initiating a trial, and then to press one key in the presence of sound, and another key when no sound was presented. Hits and correct rejections were rewarded, misses and false alarms were punished with an air blast to the face from behind the keys. N=1.

3- Same method as #2 except that an adaptive tracking psychophysical method was used. N=1.

4- Same as #3. N=1.

5- Operant conditioning ("go, no-go") for a food reward using a tracking procedure. Data are for two animals. The data plotted here are from Fig. 1 of a review paper by Watkins and Wartzok (1985) who obtained the data through personal communication from Schusterman and Moore.

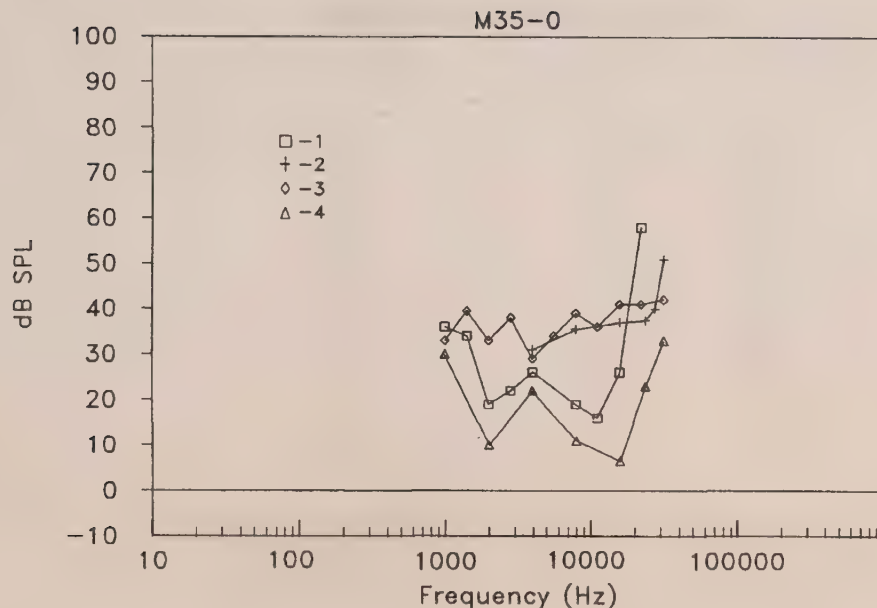


Fig. M35-0. In-air audiograms for several pinnipeds.

- 1- *Phoca vitulina vitulina* - common harbor seal (Mohl, 1968)
- 2- *Zalophus californianus* - California sea lion (Schusterman, 1974)
- 3- *Pagophilus groenlandicus* - harp seal (Terhune and Ronald, 1971)
- 4- *Callorhinus ursinus* - Northern fur seal (Schusterman and Moore, 1980)

References:

- Mohl, B. (1968) Auditory sensitivity of the common seal in air and water. *J. Aud. Res.* 8, 27-38.
- Schusterman, R.J. (1974) Auditory sensitivity of the California sea lion to airborne sound. *J. Acoust. Soc. Amer.* 56, 1248-1251.
- Schusterman, R.J., and Moore, P.W.B. (1980) Auditory sensitivity of northern fur seals (*Callorhinus ursinus*) and a California sea lion (*Zalophus californianus*) to airborne sound. *J. Acoust. Soc. Amer.* 68, S6 (abstract). Cited in Watkins, W.A., and Wartzok, D. (1985) Sensory biophysics of marine mammals. *Marine Mammal Science* 1, 219-260.
- Terhune, J.M., and Ronald, K. (1971) The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777), X. The air audiogram. *Can. J. Zool.* 49, 385-390.

Table M35-0. In-air audiograms for several pinnipeds.

Frequency (Hz)	dB SPL			
	1	2	3	4
1000	36		33	30
1420	34		39	
2000	19		33	10
2830	22		37	
4000	26	31	29	22
5600			34	
8000	19	35.5	38	11
11250	16		35	
16000	26	37	41	6.5
22500	58		41	
24000		37.5		23
28000		40		
32000		51	42	33

Notes:

1- Operant conditioning with a food reward using the method of constant stimuli. Animals were trained to make a response initiating a trial, and then to press one key in the presence of sound, and another key when no sound was presented. Hits and correct rejections were rewarded, misses and false alarms were punished with an air blast to the face from behind the keys. N=1.

2- Operant conditioning of a vocal response for food reward using a modified method of limits. Animals were trained to "station" at a fixed position, and to emit "click" vocalizations in the presence of a tone signal in order to receive a food reward. Tone signals had 100 msec rise/fall times. Results from a later study (Schusterman and Moore, 1980) indicated that the thresholds shown here below 24000 Hz were likely masked by ambient noise. The data from this later study are not plotted here, but can be found in Fig. 1 in the review paper by Watkins and Wartzok (1985). N=1.

3- Operant conditioning with a food reward using an adaptive tracking psychophysical procedure. Animals were trained to make a response initiating a trial, and then to press one key in the presence of sound, and another key when no sound was presented. Hits and correct rejections were rewarded, misses and false alarms were punished with an air blast to the face from behind the keys. N=1.

4- Operant conditioning ("go, no-go") for a food reward using a tracking procedure. Data are for two animals. The data plotted here are from Fig. 1 of a review paper by Watkins and Wartzok (1985) which they obtained by personal communication from Schusterman and Moore.

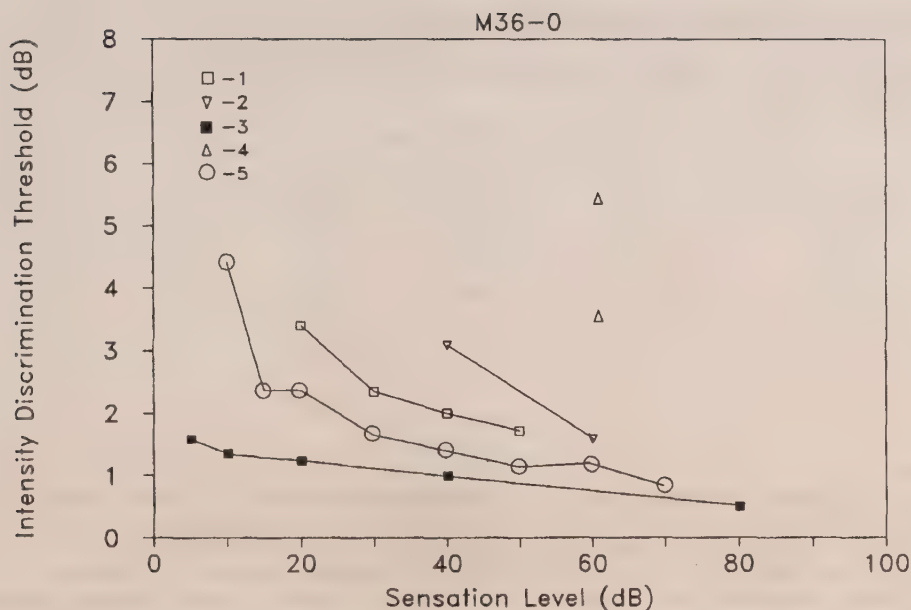


Fig. M36-0. Intensity discrimination as a function of sound level in primates.

- 1- Subfamily Cercopithecinae - Old World monkey (Sinnott, Petersen, and Hopp, 1985)
- 2- Subfamily Cercopithecinae - Old World monkey (Stebbins, Pearson, and Moody, 1969)
- 3- *Homo sapiens* - human (Jesteadt, Wier, and Green, 1977)
- 4- *Homo sapiens* - human infant (Sinnott and Aslin, 1985)
- 5- *Macaca mulatta* - rhesus monkey (Clopton, 1972)

References:

- Clopton, B.M. (1972) Detection of increments in noise intensity by monkeys. *J. Exp. Anal. Behav.* 17, 473-481.
- Jesteadt, W., Wier, C.C., and Green, D.M. (1977) Intensity discrimination as a function of frequency and level. *J. Acoust. Soc. Amer.* 61, 169-177.
- Stebbins, W.C. Pearson, R.D., and Moody, D.B. (1969) Hearing in the monkey (*Macaca*): Absolute and differential sensitivity. *J. Acoust. Soc. Amer.* 46, S20, abstract. (Manuscript circulated following presentation.)
- Sinnott, J. M. and Aslin, R.N. (1985) Frequency and intensity discrimination by human infants. *J. Acoust. Soc. Amer.* 78, 1986-1992.
- Sinnott, J.M., Petersen, M.R., and Hopp, S.L. (1985) Frequency and intensity discrimination in humans and monkeys. *J. Acoust. Soc. Amer.* 78, 1977-1985.

Table M36-0. Intensity discrimination as a function of sound level in primates.

Sensation Level (dB)	Intensity Discrimination Threshold (dB)				
	1	2	3	4	5
5			1.6		
10			1.37		4.4
15					2.4
20	3.4		1.25		2.4
30	2.35				1.7
40	2	3.1	1.01		1.45
50	1.72				1.2
60		1.6		3.6	1.25
60				5.4	
70					0.9
80			0.52		

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli. Animals made and maintained an observing response until a signal (tone bursts alternating in intensity) was presented. Signals were 250 msec duration 1 kHz tones with 10 msec rise/fall times repeating twice per sec. Individual psychometric functions are given. Earphones were used. Subjects were two *Macaca fuscata* (Japanese macaque) and one *Cercopithecus aethiops* (vervet monkey). Means: N=3.

2- Operant conditioning with a food reward using a tracking psychophysical procedure. Animals made and maintained an observing response until a signal (4 kHz tone bursts alternating in intensity) was presented. Earphones were used. Means: N=2.

3- Adaptive, two-interval, forced-choice procedure. Signals were 500 msec bursts filtered through a 200 Hz pass band centered on the signal frequency, presented at 40 dB sensation level. Data plotted are medians of intensity discrimination thresholds determined over eight frequencies from 200 to 8000 Hz. Means: N=3.

4- Operant headturning response reinforced with the opportunity to view a motorized toy bear or monkey, using a tracking procedure. Infants were 7-9 months of age. A 1 kHz tone (330 msec duration, 10 msec rise/fall times, repeated every 750 msec.) was repeated continuously, and the intensity discrimination signal consisted of an alternation of successive bursts for three sec between the standard intensity and a greater comparison intensity. Data plotted here were obtained from group psychometric functions for ten infants (5.4 dB threshold at 50% detection), and for the three best infants (3.6 dB for 50% detection). When the comparison intensity was lower than the standard intensity, the infants were unable to learn the response. Intensity discrimination thresholds for human adults were 1-1.5 dB, regardless of whether the comparison intensity was greater or less than the standard.

5- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to press a bar after a cue light onset to indicate the presence (left bar) or absence (right bar) of a 100 msec increment (10 msec rise/fall times) in a continuous noise. The sensation levels of the noise plotted and tabled are approximate (and probably accurate to within 10 dB) since the level of the noise above threshold was not measured. Thresholds were defined by a performance measure approximating $d' = 1$ in a "yes-no" task. N=1.

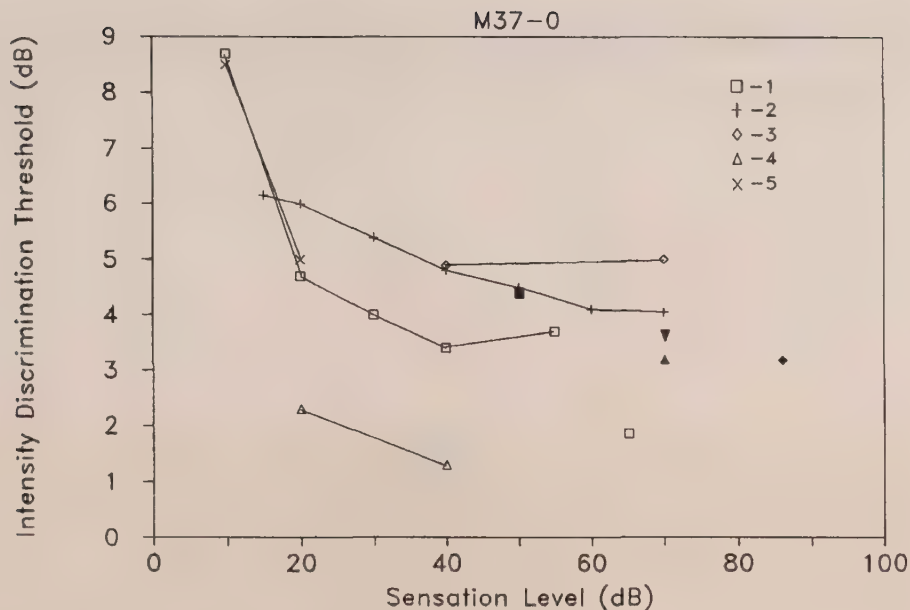


Fig. M37-0. Intensity discrimination as a function of level in several species.

- 1- *Chinchilla laniger* - chinchilla (Saunders, Shivapuja, and Salvi, 1987)
- 2- *Mus musculus* - laboratory mouse (Ehret, 1975b)
- 3- *Rattus norvegicus* - albino rat (Terman, 1970)
- 4- *Rattus norvegicus* - albino rat (Hack, 1971)
- 5- *Rattus norvegicus* - albino rat (Henry, 1938)

[Unconnected symbols are same as in Fig. M38-0.]

References:

- Ehret, G. (1975b) Frequency and intensity difference limens and nonlinearities in the ear of the housemouse (*Mus musculus*). *J. Comp. Physiol.* 102, 321-336.
- Hack, M.H. (1971) Auditory intensity discrimination in the rat. *J. Comp. Physiol. Psychol.* 74, 315-318.
- Henry, F.M. (1938) Audition in the white rat III. Absolute and relative intensity thresholds. *J. Comp. Psychol.* 26, 45-62.
- Saunders, S.S., Shivapuja, B.G., and Salvi, R.J. (1987) Auditory intensity discrimination in the chinchilla. *J. Acoust. Soc. Amer.* 82, 1604-1607.
- Terman, M. (1970) Discrimination of auditory intensities by rats. *J. Exp. Anal. Behav.* 13, 145-160.

Table M37-0. Intensity discrimination as a function of level in several species.

Sensation Level (dB)	Intensity Discrimination Threshold (dB)				
	1	2	3	4	5
10	8.7				8.5
15		6.15			
20	4.7	6		2.3	5
30	4	5.4			
40	3.4	4.8	4.9	1.3	
50		4.5			
55	3.7				
60		4.1			
70		4.05	5		

Notes:

1- Operant conditioning for a food reward using a tracking psychophysical procedure. Animals were trained to make an observing response by pressing a bar. Reward could be gained only by releasing the bar within 1.5 sec of the onset of an incremented tone. A background signal consisted of 500 msec tone bursts repeated once per sec with 5 msec rise/fall times. The conditioning signal was an alternation between two intensities between successive bursts. Data are medians over four frequencies and over three animals tested in each condition. There was no significant effect of frequency and no significant interaction between frequency and intensity.

2- Operant conditioning for a water reward using the descending method of limits. Animals learned to approach and lick a drinking tube during intensity increments. Signals were 100 msec tone bursts (10 msec rise/fall times) repeated 5 times per sec. The thresholds plotted here are averaged over nine intensity discrimination threshold functions of frequency. Means: N=11.

3- Operant conditioning for rewarding brain stimulation using the method of constant stimuli. Animals pressed one lever during a standard tone intensity, and a second lever during "comparison" tone intensity. Signal was a 4 kHz tone. Data plotted here obtained as 75% correct points on individual psychometric functions. Median: N=3.

4- Operant conditioning for a food reward using the method of constant stimuli. An animal made an observing response and remained until a continuous 8 kHz tone was incremented in intensity. A response within 1.2 sec was reinforced. Means: N=5.

5- Two-choice discrimination in a "Y" maze using the descending method of limits. A response to the incorrect arm was punished with shock. Simultaneous, continuous signals from the ends of both arms of the maze. The animal was trained to go to the higher intensity. Means: N=15.

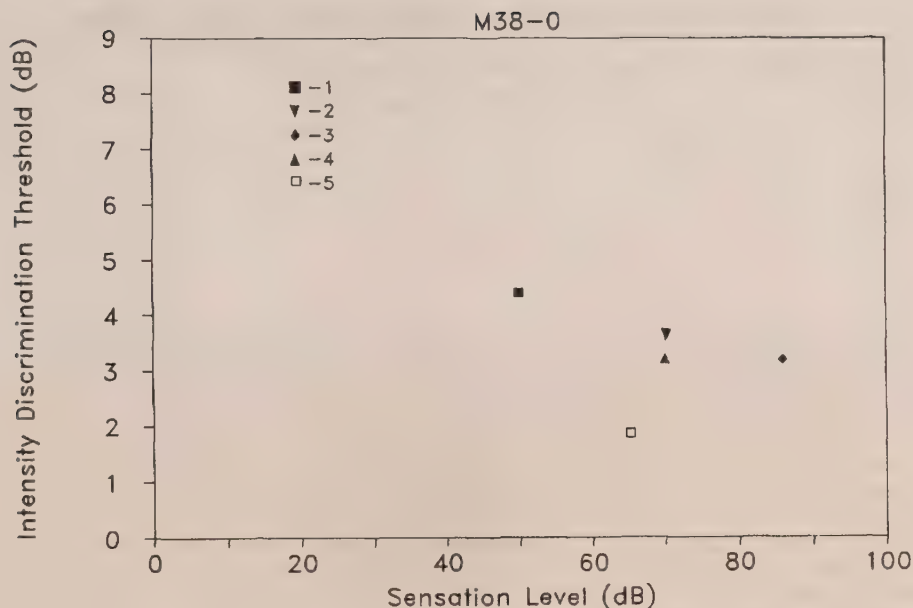


Fig. M38-0. Intensity discrimination as a function of level in several species.

- 1- *Felis catus* - cat (Saunders, 1969)
- 2- *Felis catus* - cat (Igarashi, Cranford, Allen, and Alford, 1979)
- 3- *Cavia procellus* - guinea pig (Prosen, Moody, Stebbins, and Hawkins, 1981)
- 4- *Zalophus californianus* - California sea lion (Moore and Schusterman, 1976)
- 5- *Felis catus* - cat (Oesterreich, Strominger, and Neff, 1971)

References:

- Igarashi, M., Cranford, J.L., Allen, E.A. and Alford, B.R. (1979) Behavioral auditory function after transection of crossed olivo-cochlear bundle in the cat. *Acta Otolaryngol.* 87, 429-433.
- Moore, P.W.B., and Schusterman, R.J. (1976) Discrimination of pure tone intensities by the California sea lion. *J. Acoust. Soc. Amer.* 60, 1405-1407.
- Oesterreich, R.E., Strominger, N.L., and Neff, W.D. (1971) Neural structures mediating differential sound intensity discrimination in the cat. *Brain Research* 27, 251-270.
- Prosen, C. A., Moody, D.B., Stebbins, W.C., and Hawkins, J.E. Jr. (1981) Auditory intensity discrimination after selective loss of outer hair cells. *Science*, 212, 1286-1288.
- Saunders, J.C. (1969) Behavioral discrimination of click intensity in cat. *J. Exp. Anal. Behav.* 12, 951-957.

Table M38-0. Intensity discrimination as a function of level in several species.

Sensation Level (dB)	Intensity Discrimination Threshold (dB)				
	1	2	3	4	5
50	4.4				
65					1.8
70		3.6		3.2	
86			3.19		

Notes:

1- Instrumental shock avoidance (tilt cage) using a tracking psychophysical procedure. Signals were broad band clicks repeated continuously with a period of 400 msec. The intensity difference signal consisted of clicks alternating in intensity. A group psychometric function is given. Means: N=4.

2- Instrumental shock avoidance in a double grill box using the descending method of limits. Signals were constantly repeating 10 kHz, 500 msec tone pulses at one per sec with 100 msec rise/fall times. Group psychometric functions are given. Section of the crossed olivo-cochlear bundle produced no important effects. Means: N=10.

3- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to press a report key with their nose repeatedly. After some variable number of responses, an intensity difference signal was presented, and only responses on a second, "report" key were reinforced with food. Tone bursts repeated constantly, and the signal consisted of an alternation in the intensity of successive bursts. Thresholds obtained at 8 and 16 kHz were averaged. A kanamycin induced hearing loss did not affect intensity discrimination thresholds obtained at a constant SPL. However, if signal level was raised from 20 to 70 dB SPL to maintain a constant sensation level for the hearing impaired animals, the intensity difference threshold declined 3 to 4 dB.

4- Operant conditioning for a food reward using a tracking psychophysical procedure in blocks of ten trials. Animals stationed and listened for a single tone pulse (at 16 kHz). If the tone was more intense than a "standard" (an "internal standard maintained by feedback"), the animal vocalized to obtain a reward. A signal detection analysis showed no important changes in response bias. N=1.

5- Instrumental shock avoidance in a double grill cage using a method of limits. Background stimuli were 1000 Hz tone bursts continuously presented at 65 dB SPL, 1.17 sec on, and 1.33 sec off with 200 msec rise/fall times. Positive stimulus was an increase in intensity for 15 sec. 75% correct criterion. Animals received various auditory cortex and collicular lesions which generally had the effect of raising intensity discrimination thresholds. Lesions of the brachium of the inferior colliculus had an unexpected, large effect. Means: N=9.

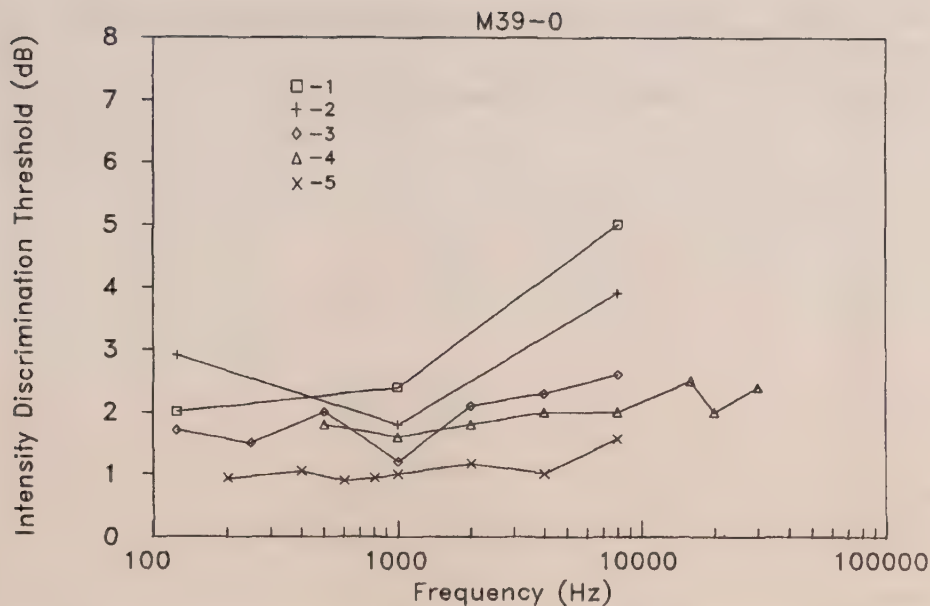


Fig. M39-0. Pure tone intensity discrimination as a function of frequency in several species.

- 1- *Felis catus* - cat (Rosenzweig, 1946)
- 2- *Felis catus* - cat (Raab and Ades, 1946)
- 3- *Felis catus* - cat (Elliot and McGee, 1965)
- 4- Subfamily Cercopithecinae - Old World monkeys (Stebbins, 1973)
- 5- *Homo sapiens* - Human (Jesteadt, Wier, and Green, 1977)

References:

- Elliot, D.N., and McGee, T.M. (1965) Effect of cochlear lesions upon audiograms and intensity discrimination in cats. *Ann. Otol. Rhinol. Laryngol.* 74, 386-408.
- Jesteadt, W., Wier, C.C., and Green, D.M. (1977) Intensity discrimination as a function of frequency and level. *J. Acoust. Soc. Amer.* 61, 169-177.
- Raab, D.H., and Ades, H.W. (1946). Cortical and midbrain mediation of a conditioned discrimination of acoustic intensities. *Amer. J. Psychol.* 59, 59-83.
- Rosenzweig, M.R. (1946) Discrimination of auditory intensities in the cat. *Amer. J. Psychol.* 59, 127-136.
- Stebbins, W.C. (1973) Hearing of old world monkeys (Cercopithecinae). *Am. J. Phys. Anthropol.* 38, 357-364.

Table M39-0. Pure tone intensity discrimination as a function of frequency in several species.

Frequency (Hz)	Intensity Discrimination Threshold (dB)				
	1	2	3	4	5
125	2	2.9	1.7		
200					0.93
250			1.5		
400					1.05
500			2	1.8	
600					0.89
800					0.93
1000	2.4	1.8	1.2	1.6	1
2000			2.1	1.8	1.17
4000			2.3	2	1.01
5000					
8000	5	3.9	2.6	2	1.57
16000				2.5	
20000				2	
30000				2.4	

Notes:

1- Instrumental shock avoidance using the descending method of limits. An animal in a rotary cage moved in the cage in order to avoid shock upon a change in sound intensity. Signals were shaped tones of 1.5 sec duration repeated every 3 sec. 40-60 dB sensation level. Means: N=3.

2- Instrumental shock avoidance using the descending method of limits. Further methods and signal specifications not given. Means: N=7.

3- Instrumental shock avoidance using the descending method of limits. Animals crossed a barrier in a double grill box in the presence of an intensity change in order to avoid shock. Signals were 400 msec tones presented every 800 msec at 60 dB sensation level. Data plotted are the mid-points of threshold ranges presented. N=12.

4- Operant conditioning for a food reward using a tracking psychophysical procedure. Animals made an observing response (hand on disk) which was held until an intensity increment occurred. Repetitive tone bursts of constant intensity were present continuously. A signal consisted of a change to bursts of alternating intensity. Data are medians of four animals representing "two genera of Cercopithecinae," most likely including *Macaca* (macaque monkeys).

5- Adaptive, two-interval, forced-choice procedure. Signals were 500 msec bursts filtered through a 200 Hz pass band centered on the signal frequency, presented at 40 dB sensation level. Thresholds were also determined similarly at 5, 10, 20, and 80 dB sensation level. Means: N=3.

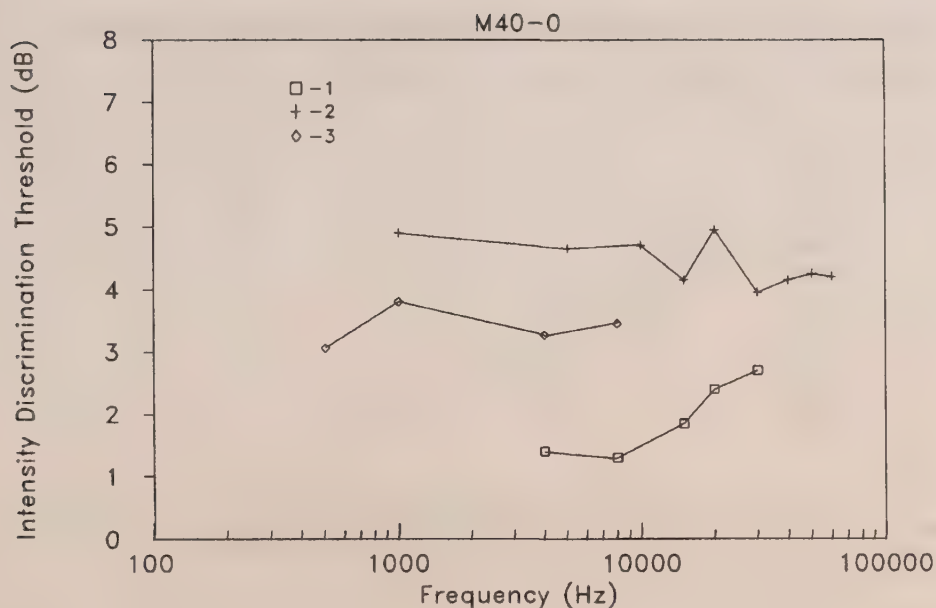


Fig. M40-0. Pure tone intensity discrimination as a function of frequency in rodents.

- 1- *Rattus norvegicus* - laboratory rat (Hack, 1971)
- 2- *Mus musculus* - laboratory mouse (Ehret, 1975b)
- 3- *Chinchilla laniger* - chinchilla (Saunders, Shivapuja, and Salvi, 1987)

References:

- Ehret, G. (1975b) Frequency and intensity difference limens and nonlinearities in the ear of the housemouse (*Mus musculus*). J. Comp. Physiol. 102, 321-336.
- Hack, M.H. (1971) Auditory intensity discrimination in the rat. J. Comp. Physiol. Psychol. 74, 315-318.
- Saunders, S.S., Shivapuja, B.G., and Salvi, R.J. (1987) Auditory intensity discrimination in the chinchilla. J. Acoust. Soc. Amer. 82, 1604-1607.

Table M40-0. Pure tone intensity discrimination as a function of frequency in rodents.

Frequency (Hz)	Intensity Discrimination Threshold (dB)		
	1	2	3
500			3.1
1000		4.9	3.8
4000	1.4		3.3
5000		4.7	
8000	1.3		3.5
10000		4.7	
15000	1.9	4.2	
20000	2.4	5.0	
30000	2.7	4.0	
40000		4.2	
50000		4.3	
60000		4.2	

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli. An animal broke a photo beam with its head (observing response) and remained until the continuous tone was incremented in intensity. A response to the increment within 1.2 sec was reinforced. 40 dB sensation level. Means: N=5.

2- Operant conditioning for a water reward using the descending method of limits. Animals learned to approach and lick a drinking tube during intensity increments. Signals were 100 msec tone bursts (10 msec rise/fall times) repeated 5 times per sec. The thresholds plotted here are interpolated (at 50 dB sensation level) from intensity discrimination threshold functions of intensity. Means: N=11.

3- Operant conditioning for a food reward using a tracking psychophysical procedure. Animals were trained to make an observing response by pressing a bar. Reward could be gained only by releasing the bar within 1.5 sec of the onset of an incremented tone. A background signal consisted of 500 msec tone bursts repeated once per sec with 5 msec rise/fall times. The conditioning signal was an alternation between two intensities between successive bursts. Data are medians over 3 animals tested at 40 dB sensation level (SL). Data were also obtained at 10, 20, 30, and 55 dB SL. There was no significant effect of frequency and no significant interaction between frequency and intensity.

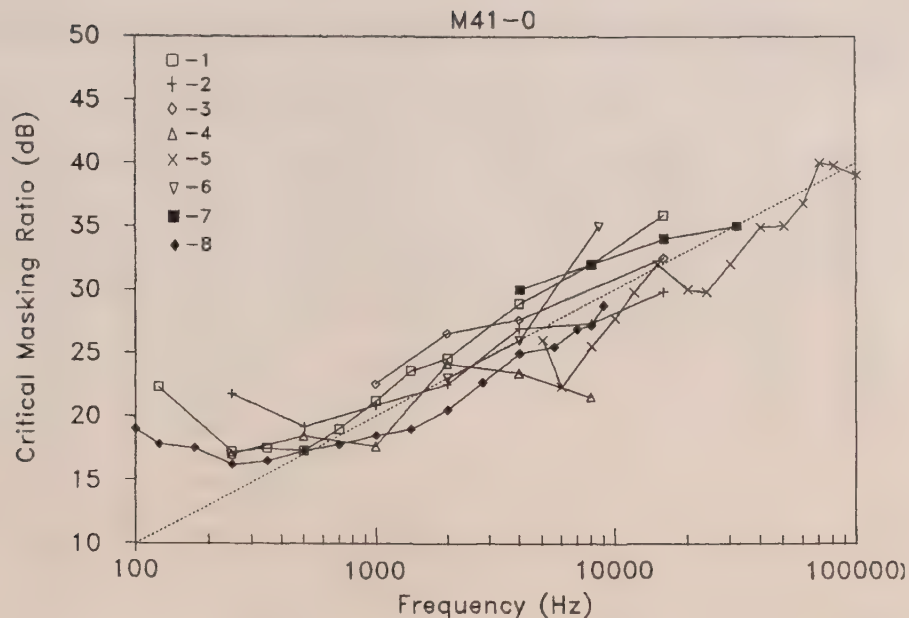


Fig. M41-0. Critical masking ratios (signal-to-noise ratios at threshold) for several mammals.

- 1- *Felis catus* - cat (Watson, 1963)
- 2- *Felis catus* - cat (Costalupes, 1983)
- 3- *Felis catus* - cat (Pickles, 1975)
- 4- *Macaca mulatta* - rhesus monkey (Clack, 1966)
- 5- *Tursiops truncatus* - bottlenose porpoise (Johnson, 1968)
- 6- *Pagophilus groenlandicus* - harp seal (Terhune and Ronald, 1971)
- 7- *Pusa hispida* - ringed seal (Terhuna and Ronald, 1975b)
- 8- *Homo sapiens* - human (Hawkins and Stevens, 1950)

References:

- Clack, T.D. (1966) Effect of signal duration on the auditory sensitivity of humans and monkeys (*Macaca mulatta*). *J. Acoust. Soc. Amer.* 40, 1140-1146.
- Costalupes, J.A. (1983) Broad band masking noise and behavioral pure tone thresholds in cats. *J. Acoust. Soc. Amer.* 74, 758-764.
- Hawkins, J.H., and Stevens, S.S. (1950) The masking of pure tones and of speech by white noise. *J. Acoust. Soc. Amer.* 22, 6-13.
- Johnson, C.S. (1968) Masked tonal thresholds in the bottle-nosed porpoise. *J. Acoust. Soc. Amer.* 44, 965-967.
- Pickles, J.O. (1975) Normal critical bands in the cat. *Acta Oto-laryngol.* 80, 245-254.
- Terhune, J.M. and Ronald, K. (1971) The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). X. The air audiogram. *Can. J. Zool.* 49, 385-390.
- Terhune, J.M., and Ronald, K. (1975b) Masked hearing thresholds of ringed seals. *J. Acoust. Soc. Amer.* 58, 515-516.
- Watson, C.S. (1963) Masking of tones by noise for the cat. *J. Acoust. Soc. Amer.* 35, 167-172.

Table M41-0. Critical masking ratios (signal-to-noise ratios at threshold) for several mammals.

Frequency in Hz, Critical Ratio (CR) in dB									
Hz	1 CR	Hz	2 CR	3 CR	Hz	4 CR	Hz	5 CR	8 CR
125	22.3	250	21.8		250	17.1	5000	26	100 19
250	17.2	500	19.2		500	18.5	6000	22.3	125 17.8
350	17.5	1000	20.9	22.6	1000	17.7	8000	25.5	175 17.5
500	17.3	2000	22.6	26.3	2000	24.2	10000	27.7	250 16.2
700	19	4000	27	27.6	4000	23.5	12000	29.8	350 16.5
1000	21.2	8000	27.4	32.5	8000	21.6	15000	32	500 17.3
1400	23.6	16000	29.9				20000	30	700 17.8
2000	24.6						24000	29.8	1000 18.5
4000	28.9						30000	32	1400 19
8000	32						40000	34.9	2000 20.5
16000	35.9						50000	35	2800 22.7
							60000	36.8	4000 25
							70000	40	5600 25.5
							80000	39.8	7000 26.9
							100000	39	8000 27.2
									9000 28.8
Hz	6 CR	Hz	7 CR						
2000	23	4000	30						
4000	26	8000	32						
8600	35	16000	34						
		32000	35						

Notes:

- 1- Instrumental shock avoidance (barrier crossing) using a modified method of limits. Masker a 1 or 2 octave band centered on the signal. These are "best estimates" of the CR using all conditions (Table II in reference). Means: N= 4 monaural cats.
- 2- Operant conditioning for food using tracking. Animals trained to make an observing response and then release the manipulandum during the signal (500 msec tone bursts, 10 msec rise/fall times). Masker was broad band noise at 23.5 dB spectrum level (SL). Above 4 kHz, CRs increase at high masking noise levels. Means: N=3.
- 3- Instrumental shock avoidance (tilt cage) up to 2 kHz, and classically conditioned suppression of licking above 2 kHz, using a tracking procedure. Signals were 169 msec tone bursts with 22 msec rise/fall times. Masker a broad band noise at 30-40 dB SPL). Means: N=6. Data also given for detecting variable bandwidth noise and multi-tone complexes (not shown here).
- 4- Instrumental shock avoidance ("single lever technique") using a tracking procedure. Signals had .10 msec rise/fall time. Earphones (monaural). Means: N=2.
- 5- Operant conditioning for a food reward using a tracking procedure. Animals were trained to swim into a small area and to make an observing response, and then to leave the area and push a second lever in the presence of a tone. Masker was broad band noise at -40 dB re: 1 dyne cm⁻² SL. Data are for one animal.
- 6- Hearing in air. Operant conditioning with a food reward using the method of constant stimuli. Animals were trained to make a response initiating a trial, and then to press one key in the presence of sound, and another key when no sound was presented. Masker was broad band noise at 35 dB SPL SL. Data are for one animal.
- 7- Hearing underwater. Same methods as #6 except that tracking was used. Maskers were "various noise bands" at -30 and -40 dB re: 1 dyne cm⁻². Means: N=2.
- 8- Method of adjustment. Wide band noise at -10 to 60 dB SPL SL. Means: N=4.

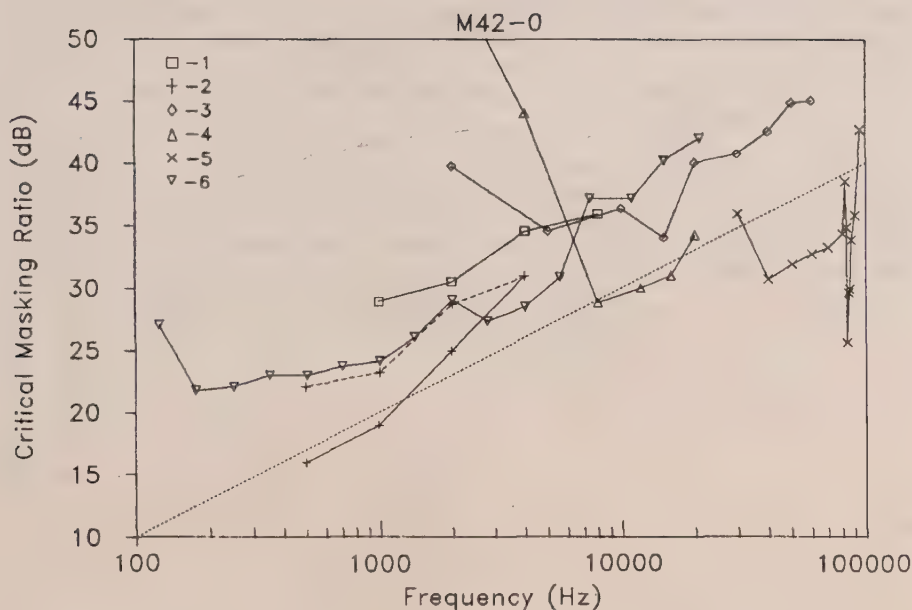


Fig. M42-0. Critical masking ratios (signal-to-noise ratios at threshold) in rodents and bats.

- 1- *Rattus norvegicus* - laboratory rat (Gourevitch, 1965)
- 2- *Chinchilla laniger* - chinchilla (Seaton and Trahiotis, 1975)
- 3- *Mus musculus* - laboratory mouse (Ehret, 1976c)
- 4- *Rousettus aegyptiacus* - fruit eating bat (Suthers and Summers, 1980)
- 5- *Rhinolophus ferrumequinum* - greater horseshoe bat (Long, 1977)
- 6- *Chinchilla laniger* - chinchilla (Miller, 1964)

Dotted line indicates a 3 dB per octave slope.

References:

- Ehret, G. (1976c) Critical bands and filter characteristics of the ear of the housemouse (*Mus musculus*). *Biol. Cybernetics* 24, 35-42.
- Gourevitch, G. (1965) Auditory masking in the rat. *J. Acoust. Soc. Amer.* 37, 439-443.
- Long, G.R. (1977) Masked auditory thresholds from the bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol.* 116, 247-255.
- Miller, J.D. (1964) Auditory sensitivity of the chinchilla in quiet and in noise. *J. Acoust. Soc. Amer.* 36, 2010 (abstract). Cited in Scharf, B. (1966) Critical Bands. Special Report LSC-S-3. Laboratory of Sensory Communication, Syracuse University.
- Seaton, W.H. and Trahiotis, C. (1975) Comparison of critical ratios and critical bands in the monaural chinchilla. *J. Acoust. Soc. Amer.* 57, 193-199.
- Suthers, R.A., and Summers, C.A. (1980) Behavioral audiogram and masked thresholds of the megachiropteran echolocating bat, *Rousettus*. *J. Comp. Physiol.* 136, 227-233.

Table M42-0. Critical masking ratios (signal-to-noise ratios at threshold) in rodents and bats.

Signal Frequency in Hz, Critical Masking Ratio (CR) in dB											
1		2		3		4		5		6	
Hz	CR	Hz	CR	Hz	CR	Hz	CR	Hz	CR	Hz	CR
1000	29	500	16	2000	39.8	2000	55.5	30000	36	125	27
2000	30.6	1000	19	5000	34.6	4000	44	40000	30.8	175	21.8
4000	34.6	2000	25	10000	36.4	8000	28.8	50000	32	250	22.1
8000	36	4000	31	15000	34.1	12000	30	60000	32.8	350	23
				20000	40.1	16000	31	70000	33.3	500	23
				30000	40.8	20000	34.2	80000	34.4	700	23.7
		500	22.1	40000	42.6			82000	38.6	1000	24.1
		1000	22.9	50000	44.9			83000	34.9	1400	26
		2000	28.9	60000	45.1			84000	25.7	2000	29
		4000	31					85000	29.7	2800	27.3
								86000	30	4000	28.4
								87000	33.9	5600	30.8
								90000	35.9	7400	37
								95000	42.8	11000	37
										15000	40
										21000	41.8

Notes:

1- Operant conditioning with a water reward using a tracking procedure. Animals pressed on one bar in the presence of a tone for water, and pressed another bar when the signal was not present. Masker was wide band noise at from 12 to 47 dB SPL spectrum level (SL). Signal had 250 msec rise/fall times. Means: N=7.

2- (Solid line: 1st measurement set. Dashed line: 2nd measurement set after more practice and a more strict criterion adopted by the animals.) Instrumental shock avoidance (jumping a barrier) using a modified method of limits. Masker was wide band noise at 5, 15, and 25 dB SPL spectrum level. Signal was 750 msec tone burst with 50 msec rise/fall times. Means: N=6 monaural animals.

3- Classical conditioning of eyelid reflex using a modified method of limits. Masker was wide band noise at 0 and 20 dB SPL spectrum level. Signal was 1000 msec tone burst with 100 msec rise/fall times. See Ehret (1977) for a study of the development of masking effects in mouse pups. Means: N=9.

4- Operant conditioning for a food reward using the descending method of limits. Animal trained to hang from the ceiling of its cage as an observing response, and to wait a variable period for a tone presentation. If the animal left its platform and went to a feeding area within five sec of the tone presentation, it was rewarded with a piece of fruit. Masker was wide band noise at 31.7 dB SPL spectrum level. Signals were 100 msec tone bursts with 20 msec rise/fall times repeated twice per sec. N=1.

5- Classical cardiac conditioning using the staircase psychophysical procedure. Restrained animals received a six sec conditioned stimulus consisting of 30 msec tone pulses repeated 10 per sec with rise fall times from 0.5 to 10 msec. An air puff to the face or electric shock was the unconditioned stimulus. Masker was wide band noise at 25 dB SPL spectrum level. Signal was 30 msec tone bursts with 0.5 msec rise/fall times presented 10 per sec. Means: N=3.

6- These data have not been published by Miller to my knowledge, but have been included in reviews of CR data several times (e.g. Gourevitch, 1970). Experimental conditions likely those of Fig. M16-0, #1 (Miller, 1970). These data were taken from a review by Scharf (1966).

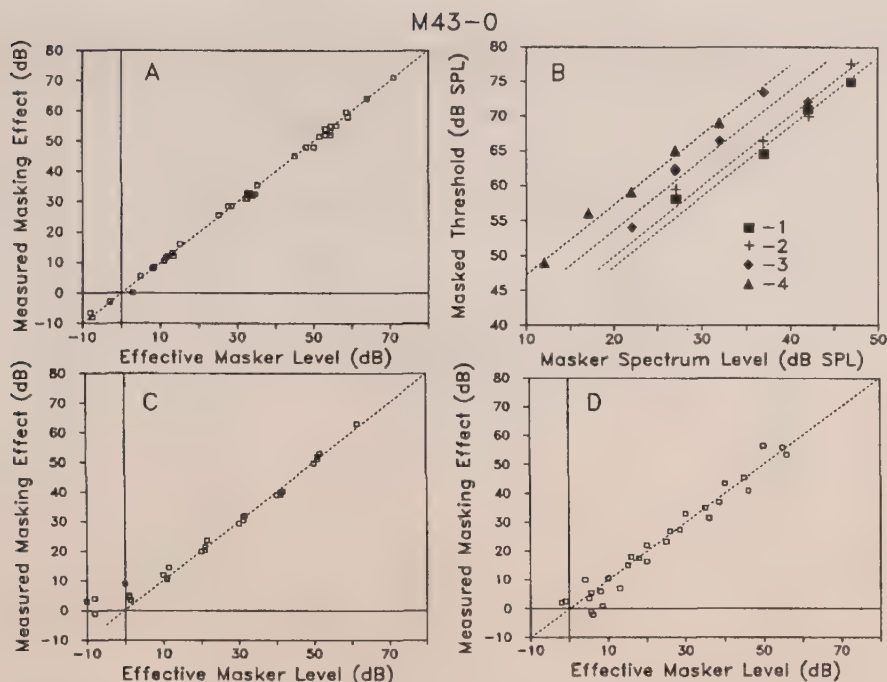


Fig. M43-0. Masked threshold as a function of masker level in several mammal species.

- A- *Mus musculus* - house mouse (Ehret, 1975a)
 B- *Rattus norvegicus* - albino rat (Gourevitch, 1965)
 1- 1000 Hz signal frequency
 2- 2000 Hz signal frequency
 3- 4000 Hz signal frequency
 4- 8000 Hz signal frequency
 C- *Felis catus* - cat (Watson, 1963)
 D- *Tursiops truncatus* - bottlenose porpoise (Johnson, 1968)

References:

- Ehret, G. (1975a) Masked auditory thresholds, critical ratios, and scales of the basilar membrane of the housemouse (*Mus musculus*). *J. Comp. Physiol.* 103, 329-341.
 Gourevitch, G. (1965) Auditory masking in the rat. *J. Acoust. Soc. Amer.* 37, 439-443.
 Johnson, C.S. (1968) Masked tonal thresholds in the bottle-nosed porpoise. *J. Acoust. Soc. Amer.* 44, 965-967.
 Watson, C.S. (1963) Masking of tones by noise for the cat. *J. Acoust. Soc. Amer.* 35, 167-172.

Table M43-0. Masked threshold as a function of masker level in several mammal species.

Effective Masker Level (dB _{ml}), and Masking Effect (dB _{me})										
	A		B1	B2	B3	B4		C		D
dB _{ml}	dB _{me}	dB _{ml}	dB _{me}	dB _{me}	dB _{me}	dB _{me}	dB _{ml}	dB _{me}	dB _{ml}	dB _{me}
							-10	3		
-8	-6.5	12				49	-8	-1	-2	2
7.5	-8	17				56	-8	4	-1	2.5
-3	-3	22			54	59	0	9	4	10
3	0	27	58	59.5	62.5	65	1	5	5	3.5
5	5.5	32			66.5	69	1	4.5	5.5	5.5
8	8	37	64.5	66.5	73.5		1.5	3.5	5.5	-1
8.5	8.5	42	71	70	72		10	12	6	-2
11	10.5	47	75	77.5			11	11	8	6
11.5	11.5						11	10.5	8.5	1
12	12						11.5	14.5	10	10.5
13	13						20	20	13	7
13.5	12						21	21.5	15	15
15	16						21	20.5	16	18
25	25.5						21.5	23.8	18	17.5
27.5	28.5						30	29.5	20	16.5
28.5	28.5						31	31.7	20	22
32	31						31	30.5	25	23.5
32.5	31						31.5	32	26	27
32.5	33						40	39	28.5	27.5
33	33						41	39.2	30	33
33	32						41	40	35	35
34	32						41.5	40.2	36	31.5
34.5	32.5						50	49.8	38.5	37
35	35.5						51	52	40	43.5
45	45						51	51	45	45.5
48	48						51.5	53	46	41
50	48						61.5	63	50	56.5
51.5	51.5								55	56
53	52									
53	54									
54.5	52									
54.5	53									
54.5	55									
56	55									
58.5	59.5									
59	58									
64	64									
71	71									

Notes:

See Hawkins and Stevens (1950) for similar data for the human.

Dashed lines indicate unity slope.

A- See Notes for Fig. M42-0, #3. Effective masker level is defined as the CR (in dB) plus the masker spectrum level minus the threshold in quiet (in dB).

B- See Notes for Fig. M42-0, #1. Masker spectrum level.

C- See Notes for Fig. M42-0, #1. Effective masker level as in A.

D- See Notes for Fig. M42-0, #5. Effective masker level as in A.

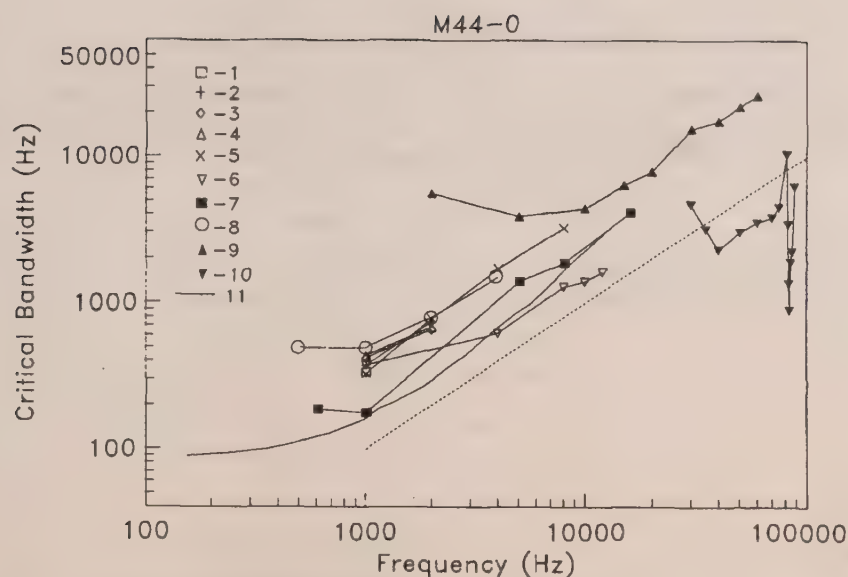


Fig. M44-0. Critical Bandwidths determined for several mammals.

- 1- *Felis catus* - cat (Pickles, 1976) 2-4- *Felis catus* - cat (Pickles, 1979)
 5- *Felis catus* - cat (Pickles, 1975) 6- *Felis catus* - cat (Nienhuys and Clark, 1979)
 7- *Macaca nemestrina* - pig-tailed macaque (Gourevitch, 1971)
 8- *Chinchilla laniger* - chinchilla (Seaton and Trahiotis, 1975)
 9- *Mus musculus* - house mouse (Ehret, 1976c)
 10- *Rhinolophus ferrumequinum* - greater horseshoe bat (Long, 1980)
 11- *Homo sapiens* - human (Zwicker, Flottorp, and Stevens, 1959)

- Ehret, G. (1976c) Critical bands and filter characteristics of the ear of the housemouse (*Mus musculus*). *Biol. Cybernetics* 24, 35-42.
- Gourevitch, G. (1970) Detectability of tones in quiet and in noise by rats and monkeys. In Stebbins, W.C. (ed) *Animal Psychophysics: The Design and Conduct of Sensory Experiments*. Appleton-Century-Crofts: New York, pp. 67-97.
- Long, G. (1980) Some psychophysical measurements of frequency processing in the greater horseshoe bat. In van der Brink, G., and Bilsen, F.H. (eds), *Psychophysical, Physiological, and Behavioral Studies in Hearing*. Delft University Press: Delft, pp. 132-135.
- Nienhuys, T.W., and Clark, G.M. (1979) Critical bands following the selective destruction of cochlear inner and outer hair cells. *Acta Oto-Laryngol.* 88, 350-358.
- Pickles, J.O. (1975) Normal critical bands in the cat. *Acta Oto-laryngol.* 80, 245-254.
- Pickles, J.O. (1976) Role of centrifugal pathways to cochlear nucleus in determination of critical bandwidth. *J. Neurophysiol.* 39, 394-400.
- Pickles, J.O. (1979) Psychophysical frequency resolution in the cat as determined by simultaneous masking and its relation to auditory-nerve resolution. *J. Acoust. Soc. Amer.* 66, 1725-1732.
- Seaton, W.H. and Trahiotis, C. (1975) Comparison of critical ratios and critical bands in the monaural chinchilla. *J. Acoust. Soc. Amer.* 57, 193-199.
- Zwicker, E., Flottorp, G., and Stevens, S. (1957) Critical bandwidths in loudness summation. *J. Acoust. Soc. Amer.* 29, 548-557.

Table M44-0. Critical Bandwidths determined for several mammals.

Signal Frequency (F) in Hz or kHz, Critical Bandwidth (CB) in Hz or kHz													
F	CB									F	CB	F	CB
kHz	Hz	Hz	Hz	Hz	Hz	Hz	Hz	Hz	Hz	kHz	kHz	kHz	Hz
	1	2	3	4	5	6	7	8	9		10		11
.5								500		30	4.6	.065	90
.6							186			35	3.1	.155	90
1	336	376	436	436	350	370	176	500		40	2.3	.25	95
2		740	658	684	700			800	5611	50	3.0	.345	100
4						615		1500		60	3.5	.45	108
5							1387		3888	70	3.8	.56	120
8					1520	1288	1860			75	4.4	.69	130
10						1388			4444	81.5	10.3	.83	145
12						1613				82.5	3.4	.98	160
15									6388	83	1.3	1.155	190
16					3720		4062			83.5	.9	1.355	210
20									7944	84.5	1.9	1.580	240
30									15667	86	2.2	1.835	270
40									17772	88	6.1	2.130	320
50									22333			2.480	380
60									26444			2.900	450
												3.400	560
												4.020	680
												4.780	840
												5.700	1000
												6.850	1300
												8.400	1800
												10.500	2400
												13.300	3300

Notes:

- 1- Methods as in M41-0, #3. Masker band pass noise of variable width centered geometrically on signal. Signal a 160 msec tone, 22 msec r/f. Means: N=5 monaural cats.
- 2- Methods as above. Masker two tones centered geometrically on signal. Signal 50 Hz-wide noise band. Means: N=4
- 3- Methods as above. Masker band pass noise of variable width centered on signal. Signal a 150 msec tone, 22 msec r/f. Means: N=4.
- 4- Methods as above. Masker "rippled noise" (see Fig. F55-0). Thresholds measured at peaks and troughs of spectrum as a function of ripple density. Means: N=6.
- 5- Methods as in M41-0, #3. Masker band pass noise of variable width centered on signal. Means: N=6.
- 6- Classical conditioning of lick suppression using tracking. Masker variable bandwidth noise centered on signal. Signal 700 msec bursts, 2.5 msec r/f. Means: N=4.
- 7- Operant conditioning for food using constant stimuli. Earphones. Masker variable bandwidth noise (1 and 5 kHz) or two tones centered on signal. Medians: N=2.
- 8- Methods as in M42-0, #2. Masker variable bandwidth noise centered on signal. Signal tone had 50 msec r/f. Means: N=6.
- 9- Methods as in M42-0, #1. Masker variable bandwidth noise. Signal tone with 250 msec r/f. Means: N=9.
- 10- Methods as in M42-0, #5. Masker either variable bandwidth noise or two tones centered on signal. Signal as in M42-0, or 100 Hz-wide noise. Medians: N=2.
- 11- Loudness estimates as a function of the bandwidth of noise with indicated center frequency defined the critical band. Data from Table I of reference.

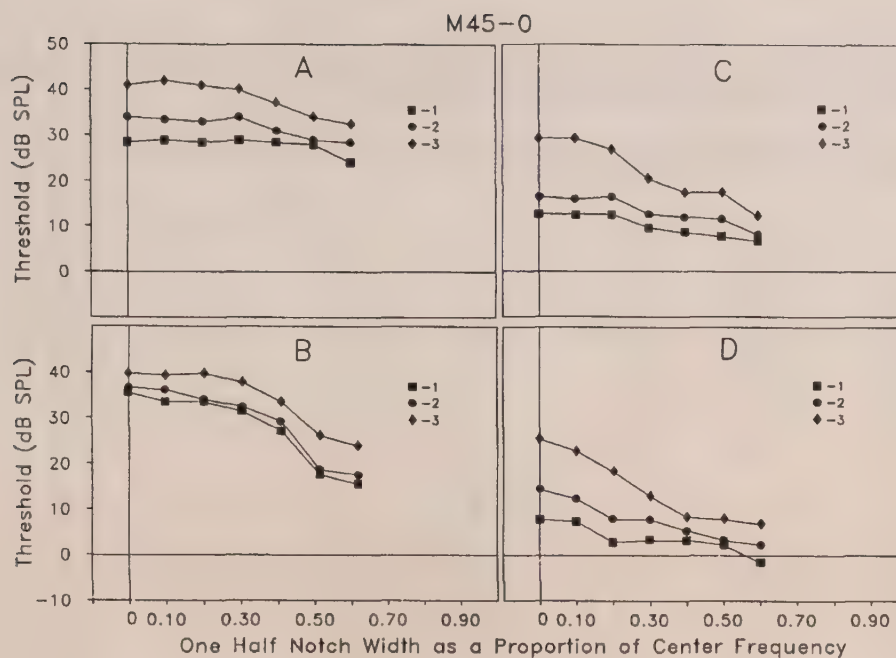


Fig. M45-0. Tone threshold as a function of masker noise notch width centered on the signal frequency in *Chinchilla laniger* (chinchilla).

A- Animal 2, 1 kHz signal

Masker spectrum level in dB SPL: 1- 25; 2- 35; 3- 45 dB

B- Animal 3, 1 kHz signal

Masker spectrum level in dB SPL: 1- 25; 2- 35; 3- 45 dB

C- Animal 2, 10 kHz signal

Masker spectrum level in dB SPL: 1- 20; 2- 30; 3- 40 dB

D- Animal 3, 10 kHz signal

Masker spectrum level in dB SPL: 1- 20; 2- 30; 3- 40 dB

Reference:

Halpern, L., and Dallos, P. (1986) Auditory filter shapes in the chinchilla. *J. Acoust. Soc. Amer.* 80, 765-775.

Table M45-0. Tone threshold as a function of masker noise notch width centered on the signal frequency in *Chinchilla laniger* (chinchilla).

NW = One Half the bandwidth of the masker notch as a proportion of the notch center frequency. Thresholds are in dB SPL.

NW	A			B		
	1	2	3	1	2	3
0	28.5	34	41	35	36	39
0.1	29	33.5	42	33	35.5	38.5
0.2	28.5	33	41	33	33.5	39
0.3	29	34	40	31	32	37
0.4	28.5	31	37	27	29	33
0.5	28	29	34	18	19	26
0.6	24	28.5	32.5	16	18	24

NW	C			D		
	1	2	3	1	2	3
0	13	17	30	7.5	14	25
0.1	13	16.5	30	7	12	22.5
0.2	13	17	27.5	2.5	7.5	18
0.3	10	13	21	3	7.5	12.5
0.4	9	12.5	18	3	5	8
0.5	8	12	18	2	3	7.5
0.6	7	8.5	12.5	-2	2	6.5

Notes:

Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to make an observing response, wait for a signal to occur, and to release the manipulandum during the signal presentation. Maskers were wide band noises with a "notch," or minimum, centered on the tone signal frequency. The notched noise was created by high-pass filtering wide band noise, and then multiplying the filtered noise by a sinusoid of either 1000 or 10000 Hz. The two flanking bands of noise produced as the output of the multiplier are the side-bands in sinusoidal amplitude modulation. The carrier sinusoid was suppressed. Signals were 10 msec tone bursts (between the 6-dB down points), with 10 msec rise/fall times, repeated once per sec. The signal followed the masker by 12.5 msec (forward masking). Signals were equal in frequency to the center of the notch, and signal thresholds were measured as a function of the width of the notch in the masker noise.

The data given here for two animals show that signal threshold declines as the notch widens. This is expected given the assumption that bandpass filters centered on the signal frequency underlie masked tone detection. Monotonic transformations of the above threshold functions were differentiated (slope calculated) and plotted as a function of relative notch width. These resulting functions are termed "auditory filter shapes." Based on these data for the chinchilla, these filter shapes have local minima (poor sensitivity) at the center frequency, and local maxima (greatest sensitivity) at a notch width about 0.5 to 0.6 times the center frequency. This unlikely filter shape results from the fact that the slopes of the functions plotted above are near zero with small inflection points at the narrower notch widths.

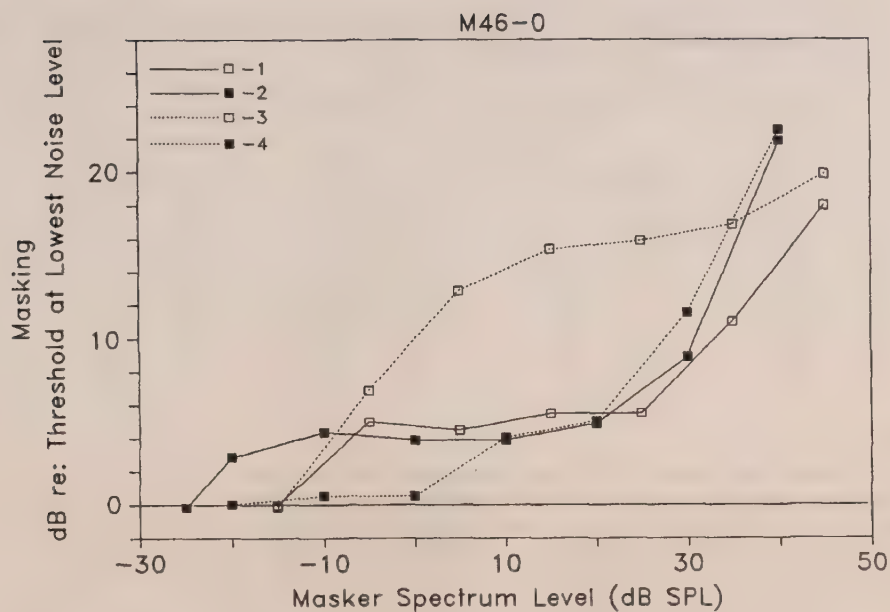


Fig. M46-0. Tone threshold in forward masking as a function of wide band masker noise level in *Chinchilla laniger* (chinchilla).

- 1- Animal 2, 1 kHz signal
- 2- Animal 2, 10 kHz signal
- 3- Animal 3, 1 kHz signal
- 4- Animal 3, 10 kHz signal

Reference:

Halpern, L. and Dallos, P. (1986) Auditory filter shapes in the chinchilla. *J. Acoust. Soc. Amer.* 80, 765-775.

Table M46-0. Tone threshold in forward masking as a function of wide band masker noise level in *Chinchilla laniger* (chinchilla).

Masker Spectrum Level in dB SPL (ML); Signal Threshold in dB SPL (ST)

1		2		3		4	
ML	ST	ML	ST	ML	ST	ML	ST
-15	23	-25	8	-15	19	-20	2.5
-5	28	-20	11	-5	26	-10	3
5	27.5	-10	12.5	5	32	0	3
15	28.5	0	12	15	34.5	10	6.5
25	28.5	10	12	25	35	20	7.5
35	34	20	13	35	36	30	14
45	41	30	17	45	39	40	25
		40	30				

Notes:

Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to make an observing response, wait for a signal to occur, and to release the manipulandum during the signal presentation. Masker was 20 kHz low pass noise at the indicated levels. Signals were 10 msec tone bursts (between the 6-dB down points), with 10 msec rise/fall times, repeated once per sec. The signal followed the masker by 12.5 msec (forward masking). Animals had one ear destroyed.

The above data were used in the study of auditory filter shapes in the chinchilla in order to transform the thresholds of Fig. M45-0 into equivalent spectrum levels of flat-spectrum noise. Note that these forward masking functions of masker level are quite non-linear compared with the functions usually obtained in simultaneous masking.

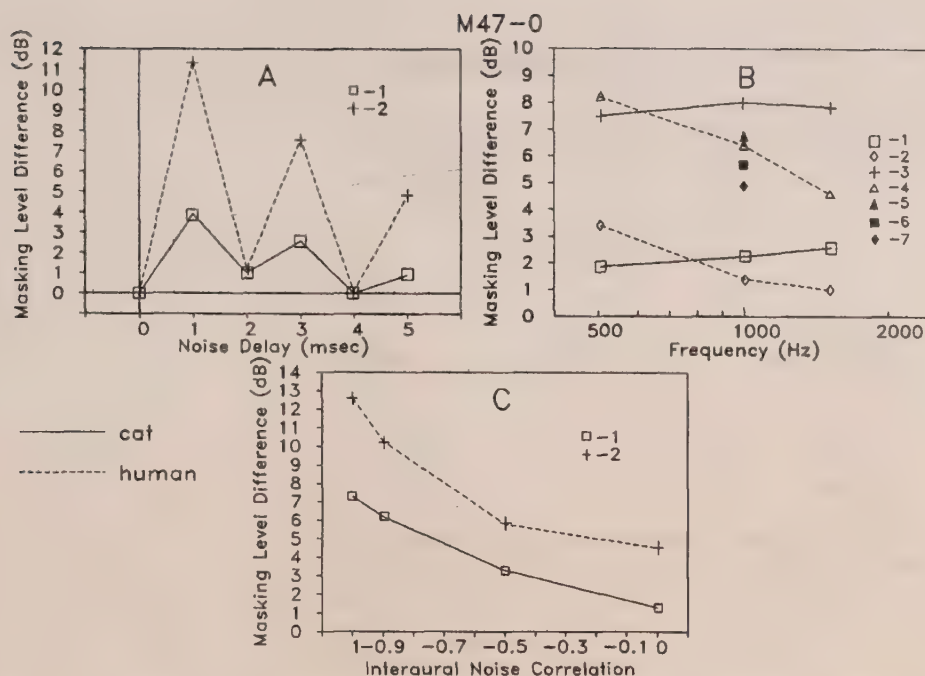


Fig. M47-0. Aspects of the binaural masking level difference (MLD) in cat and human.

A. 500 Hz detection as a function of interaural noise delay (Hoppe and Langford, 1974)

- 1- *Felis catus* - cat
- 2- *Homo sapiens* - human

B. MLD as a function of signal frequency

- 1- N_oS_o vs N_oS_m - cat (Wakeford and Robinson, 1974a)
- 2- N_oS_o vs N_oS_m - human (Wakeford and Robinson, 1974a)
- 3- N_oS_o vs N_oS_{pi} - cat (Wakeford and Robinson, 1974a)
- 4- N_oS_o vs N_oS_{pi} - human (Wakeford and Robinson, 1974a)
- 5- N_oS_o vs N_oS_{pi} - cat (Cranford, Stramler, and Igarashi, 1978)
- 6- N_mS_m vs N_oS_m - cat (Cranford, 1977)
- 7- N_mS_m vs N_oS_m - cat (Cranford, Stramler, and Igarashi, 1978)

C. Diotic detection function of interaural noise correlation (Geesa and Langford, 1976)

- 1- *Felis catus* - cat
- 2- *Homo sapiens* - human

References:

- Cranford, J.L. (1977) Auditory masking level-differences in the cat. *J. Comp. Physiol. Psychol.* 89, 219-223.
- Cranford, J.L., Stramler, J., and Igarashi, M. (1978) Role of neocortex in binaural hearing in cat III. Binaural masking-level difference. *Brain. Res.* 151, 381-385.
- Geesa, B.H., and Langford, T.L. (1976) Binaural interaction in cat and man. II. Interaural noise correlation and signal detection. *J. Acoust. Soc. Amer.* 59, 1195-1196.
- Hoppe, S.A., and Langford, T.L. (1974) Binaural interaction in cat and man. I. Signal detection and noise cross correlation. *J. Acoust. Soc. Amer.* 55, 1263-1265.
- Wakeford, O.S., and Robinson, D.E. (1974a) Detection of binaurally masked tones by the cat. *J. Acoust. Soc. Amer.* 56, 952-956.

Table M47-0. Aspects of the binaural masking level difference in cat and man.

TABLE A

Noise Delay (msec)	Masking Level Difference (dB)	
	1	2
1	3.9	11.4
2	1	1.2
3	2.6	7.6
4	0	0.1
5	0.9	4.8

TABLE B

Frequency (Hz)	Masking Level Difference (dB)						
	1	2	3	4	5	6	7
500	1.9	7.5	3.4	8.2			
1000	2.2	8	1.4	6.4	6.7	5.7	4.9
1500	2.5	7.8	1	4.6			

TABLE C

Interaural Noise Correlation	Masking Level Difference (dB)	
	1	2
-1	7.3	12.6
-0.9	6.2	10.3
-0.5	3.3	5.8
0	1.3	4.5

Notes:

The masking level difference (MLD) is a release from masking which can occur when the signal and effective masker have different interaural phase relations, relative to the cases in which they are identical at the two ears (diotic or N_oS_o), or are at one ear only (monaural, or N_mS_m). For cat, MLDs are largest for N_oS_o vs N_oS_{pi} conditions, intermediate for N_mS_m vs N_oS_m , and smallest for N_oS_o vs N_oS_m . MLD is smaller for cats than in the human, suggesting wider binaural critical bands for the cat. Cat MLDs extend to higher frequencies than in the human.

A. Shock avoidance (triple grill box) using constant stimuli. Signal 500 Hz tone with 25 msec r/f. Insert earphones kept in place with leather helmet. Masker: 100 to 1200 Hz noise band at 50 dB spectrum level. Thresholds measured as a function of the interaural delay of noise. At zero delay, the noise is diotic, and at 1 msec delay, the noise in a narrow band at 500 Hz is effectively inverted in phase interaurally (N_oS_{pi}). As delay increases, the noise becomes less correlated, even at integer multiples of the signal period. Means: N=2 cats and 2 humans tested using same earphones.

B1-B4- Same methods as in A. Signal: 50 msec r/f. Noise: 44 to 50 dB spectrum level. Relative to diotic signal and masker (N_oS_o), masking release occurred for signal monaural (N_oS_m), or phase-reversed (N_oS_{pi}) signal. Means: N=4 cats, 2 humans.

B5-B7- Essentially the same methods as in A.

B5- N_oS_o vs N_oS_{pi} . Signal 500 msec, 100 msec r/f. Means: N=9 cats.

B6- MLD defined for diotic noise and monaural signal (N_oS_m) relative to monaural masker and signal condition (N_mS_m). MLD increased 4.6 dB when 10 dB more intense noise added to other ear. Means: N=3 cats (best animals).

B7- Same signal and method as in B6. Means: N=6 cats.

C. Same methods as A. 500 Hz signal, 1.5 sec duration, 25 msec rise/fall times in phase at the two ears. Thresholds measured as a function of interaural noise decorrelation (adding independent noise to one ear). Means: N=2 cats, N=2 humans.

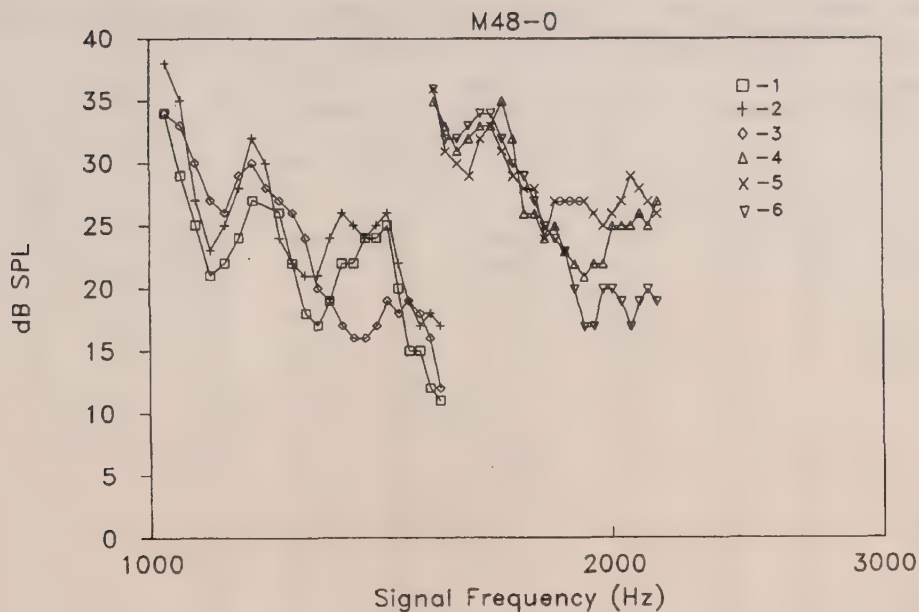


Fig. M48-0. Thresholds for tone signals in the presence of tone maskers in *Chinchilla laniger* (chinchilla) (Long and Miller, 1981).

- 1- 1000 Hz tone masker, subject 4776
- 2- 1000 Hz tone masker, subject 7176
- 3- 1000 Hz tone masker, subject 5576
- 4- 1500 Hz tone masker, subject 4776
- 5- 1500 Hz tone masker, subject 7176
- 6- 1500 Hz tone masker, subject 5576

Reference:

Long, G.L., and Miller, J.D. (1981) Tone-on-tone masking in the chinchilla. *Hear. Res.* 4, 279-285.

Table M48-0. Thresholds for tone signals in the presence of tone maskers in *Chinchilla laniger* (chinchilla) (Long and Miller, 1981).

Signal Frequency (Hz)	dB SPL			Signal Frequency (Hz)	dB SPL		
	1	2	3		4	5	6
1025	34	38	34				
1050	29	35	33	1560	35	36	36
1075	25	27	30	1590	33	31	32
1100	21	23	27	1620	31	30	32
1125	22	25	26	1650	32	29	33
1150	24	28	29	1680	33	32	34
1175	27	32	30	1710	33	33	34
1200		30	28	1740	35	31	32
1225	26	24	27	1770	32	29	30
1250	22	22	26	1800	26	28	29
1275	18	21	24	1830	26	28	27
1300	17	21	20	1860	24	24	25
1325	19	24	19	1890	25	27	24
1350	22	26	17	1920	23	27	23
1375	22	25	16	1950	22	27	20
1400	24	24	16	1980	21	27	17
1425	24	25	17	2010	22	26	17
1450	25	26	19	2040	22	25	20
1475	20	22	18	2070	25	26	20
1500	15	19	19	2100	25	27	19
1525	15	17	18	2130	25	29	17
1550	12	18	16	2160	26	28	19
1575	11	17	12	2190	25	27	20
				2220	27	26	19

Notes:

Operant conditioning for a food reward using an adaptive tracking procedure. Animals were trained to make an observing response which initiated the masker (50 dB SPL) immediately. A release of the response lever during a two sec stimulus tone presentation (occurring one to eight sec after the observing response) was rewarded. Correct rejections were rewarded also, and false alarm rates were measured to be about 5 to 20%. Sound sources for masker and signal were separate, positioned in the vertical plane at 20° and -5° respectively, relative to the right ear. Data are for three individuals.

Thresholds were also obtained at a later time with greater frequency resolution in the regions of "notches" of low threshold well above the masker frequencies. These are not plotted here. In general, these thresholds were 0 to 8 dB different (lower) from those plotted for subjects 4776 and 7176 in the region of the "notch" (2000-2100 Hz) for the 1500 Hz masker.

For both masker frequencies, the "notches" in the regions of 1100 Hz and 2100 Hz were thought to be due to the detection of the cubic difference tone ($2f_1 - f_2$, or twice the frequency of the masker minus the frequency of the signal). The authors describe these data as indicating rather poor frequency selectivity for the chinchilla in this type of masking experiment.

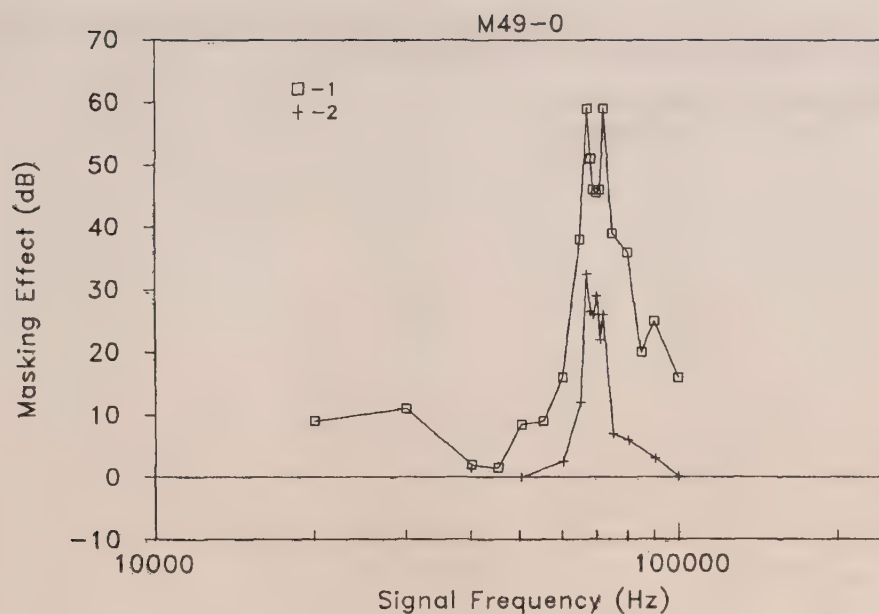


Fig. M49-0, The effect of a tone masker at 70000 Hz on the detection of tones in *Tursiops truncatus* (bottlenosed porpoise) (Johnson, 1971)

- 1- Masker 80 dB sensation level
- 2- Masker 40 dB sensation level

Reference:

Johnson, C.S. (1971) Auditory masking of one pure tone by another in the bottlenosed porpoise. J. Acoust. Soc. Amer. 49, 1317-1318.

Table M49-0. The effect of a tone masker at 70000 Hz on the detection of tones in *Tursiops truncatus* (bottlenosed porpoise) (Johnson, 1971)

Signal Frequency (Hz)	Signal Threshold (dB re: quiet case)	
	1	2
20	9	
30	11	
40	2	1.5
45	1.5	
50	8.5	0
55	9	
60	16	2.5
65	38	12
67	59	32.5
68	51	26.5
69	46	26
70	45.5	29
71	46	22
72	59	26
75	39	7
80	36	6
85	20	
90	25	3
100	16	0.2

Notes:

Operant conditioning for a food reward using a tracking procedure. Animals were trained to push a lever to initiate a trial (observing response) and to move to and press another lever when the signal was detected. Signals had rise/fall times equivalent to two or three cycles of the stimulus tone. Simultaneous masking. Maskers were pure tones at levels either 40 or 80 dB above threshold (sensation level). Data were also obtained and plotted for the 80 dB masker earlier in training, showing higher thresholds (not shown here). N=1.

The author notes that the "dips" in the function near 70000 Hz suggest beat detection, and from this calculated an intensity discrimination threshold estimate of from 0.35 to 1.0 dB.

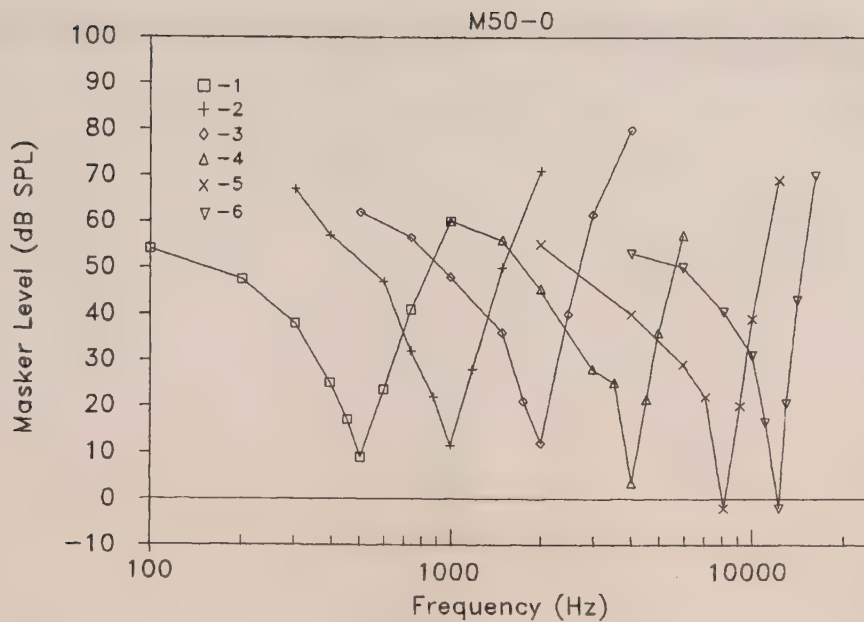


Fig. M50-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) (McGee, Ryan, and Dallos, 1976).

- 1- 500 Hz signal frequency
- 2- 1000 Hz
- 3- 2000 Hz
- 4- 4000 Hz
- 5- 8000 Hz
- 6- 12250 Hz

Reference:

McGee, T., Ryan, A., and Dallos, P. (1976) Psychophysical tuning curves of chinchillas. *J. Acoust. Soc. Amer.* 60, 1146-1150.

Table M50-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) (McGee, Ryan, and Dallos, 1976).

Frequency (Hz)	Masker Level (dB SPL)					
	1	2	3	4	5	6
100	54					
200	47.5					
300	38	67				
300	25	57				
450	17					
500	9		62			
600	23.5	47				
740	41	32	56.5			
900		22				
1000	60	11.5	48	60		
1200		28				
1500		50	36	56		
1750			21			
2000		71	12	45.5	55	
2500			40			
3000			61.5	28		
3500				25		
4000			80	3.5	40	53
4500				21.5		
4900				36		
5900				57	29	50
7000					22	
8000					-2	40.5
9100					20	
10000					39	31
11000						16.5
12250					69	-2
13000						20.5
14000						43
16100						70

Notes:

Instrumental shock avoidance (jumping a barrier) using a method of limits. The "partial forward masking" paradigm used here consisted of a repeating 120 msec pure tone masker (10 msec rise/fall times), and a 20 msec pure tone signal (10 msec rise fall times) overlapping the fall time period of the masker. (The signal began to rise at the same time the masker began to fall.) Signal fixed at 20 dB sensation level.

N=1. Data for other masking paradigms and other subjects are shown in Fig. M50-1.

For this plot, frequencies were determined from a graph (Fig. 3 in the reference) as accurately as possible, and are probably correct only to within about 2%.

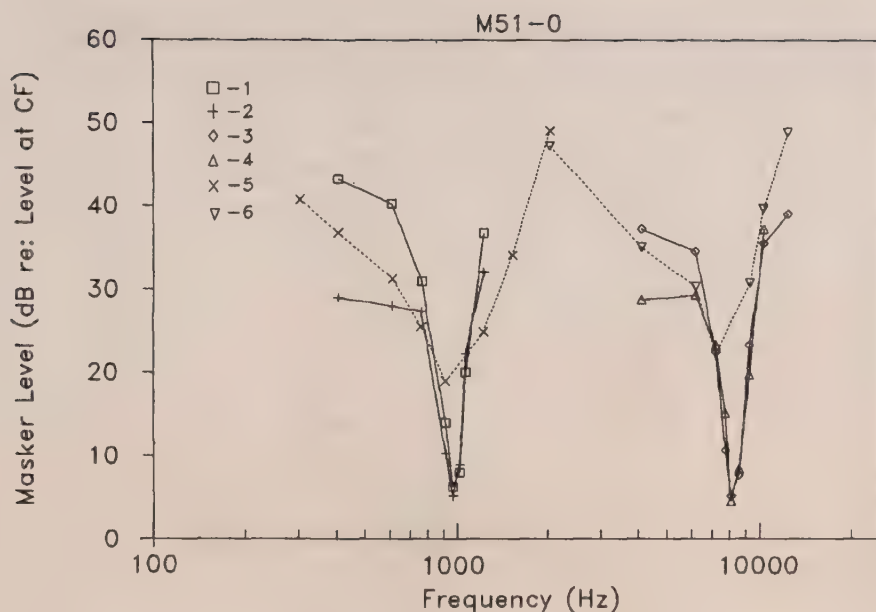


Fig. M51-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) determined in simultaneous and forward masking with signal levels at 10 and 40 dB sensation level (McGee, Ryan, and Dallos, 1976).

- 1- Forward masking, 10 dB SL signal level, 1000 Hz signal
- 2- Forward masking, 40 dB SL signal level, 1000 Hz signal
- 3- Forward masking, 10 dB SL signal level, 8000 Hz signal
- 4- Forward masking, 40 dB SL signal level, 8000 Hz signal
- 5- Simultaneous masking, 10 dB SL signal level, 1000 Hz signal
- 6- Simultaneous masking, 10 dB SL signal level, 8000 Hz signal

Reference:

McGee, T., Ryan, A., and Dallos, P. (1976) Psychophysical tuning curves of chinchillas. *J. Acoust. Soc. Amer.* 60, 1146-1150.

Table M51-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) determined in simultaneous and forward masking with signal levels at 10 and 40 dB sensation level (McGee, Ryan, and Dallos, 1976).

Masker Frequency (Hz)	Masker Level (dB re: Level at Center Frequency)					
	1	2	3	4	5	6
300					40.8	
400	43.3	29			36.8	
600	40.3	28			31.3	
750	31	27.3			25.5	
900	14	10.3			19	
950	6.3	5.2				
1000	8	9				
1050	20	22.3				
1200	36.7	32			24.9	
1500					34.1	
2000					49.1	47.3
4000			37.2	28.7		35
6000			34.5	29.3		30.3
7000			22.5	23.3		22.2
7500			10.7	15.2		
7800			5.2	4.6		
8300			7.7	8.5		
9000			23.3	19.7		30.7
10000			35.5	37.2		39.7
12000			39			48.9

Notes:

Instrumental shock avoidance (jumping a barrier) using a method of limits. In the forward masking paradigm, a repeating 120 msec pure tone masker (10 msec rise/fall times) was used with a 20 msec pure tone signal (10 msec rise fall times) which began to rise at the same time the masker had fallen to zero amplitude. In the simultaneous masking paradigm, the pure tone masker was presented continuously, and the signal was 3.8 sec in duration. Means: N=3.

In the figure above, the dashed lines indicate simultaneous masking. Since a signal was not presented at the same frequency as the masker, the curves appear truncated near the signal frequency. The authors note that there were no statistically significant differences between the curves determined at different sensation levels, or using different masking paradigms (see Fig. M50-0).

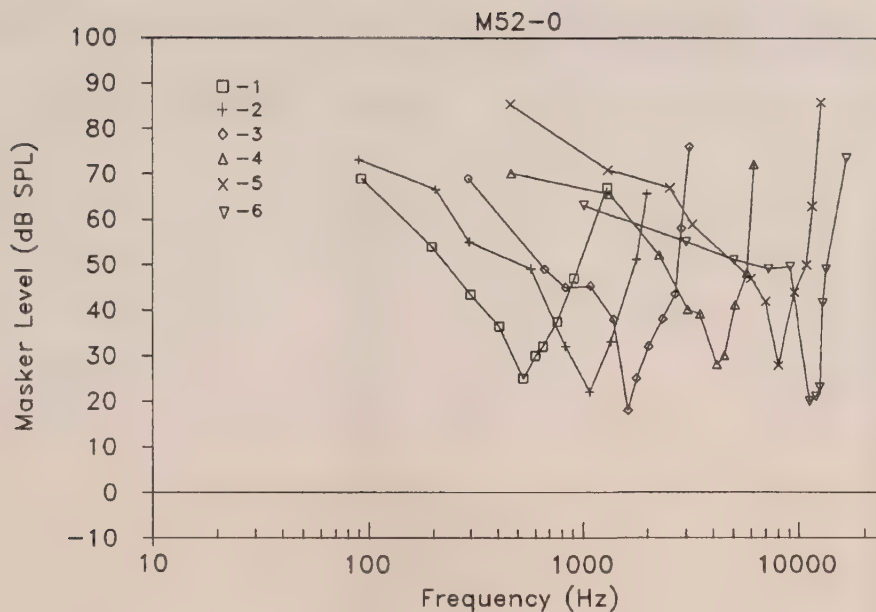


Fig. M52-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) (Salvi, Ahroon, Perry, Gunnarson, and Henderson, 1982).

- 1- 500 Hz signal frequency
- 2- 1000 Hz
- 3- 2000 Hz
- 4- 4000 Hz
- 5- 8000 Hz
- 6- 11000 Hz

Reference:

Salvi, R.J., Ahroon, W.A., Perry, J.W., Gunnarson, A.D., and Henderson, D. (1982)
Comparison of psychophysical and evoked-potential tuning curves in the chinchilla.
Am. J. Otolaryngol. 3, 408-416.

Table M52-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) (Salvi, Ahroon, Perry, Gunnarson, and Henderson, 1982).

Frequency (Hz)	Masker Level (dB SPL)						Frequency (Hz)	Masker Level (dB SPL)			
	1	2	3	4	5	6		3	4	5	6
90	69	73					2800			58	
200	54	66.5					2960				55
300	43.5	55	69				3100	76	40		
400	36.5						3200			59	
460				70	86		3500		39		
520	25						4200		28		
560		49					4500		30		
600	30						4930				51
650	32		49				5100		41		
750	37.5						5700		48		
800		32					6000			47	
825			45				6200		72		
900	47						6900			42	
1000						63	7100				49
1100		22	45.3				7900			28	
1300	67				71		8920				49
1350		33		65.5			9400			44	
1400			38				10700			50	
1600			18				11000				20
1760		51	25				11400			63	
1950		65.5					11750				21
2000			32				12200				23
2300			38	52			12500			86	
2500					67		12650				41
2670			43.5				13100				49
							16300				74

Notes:

Instrumental shock avoidance using a tracking procedure. Animals were restrained over a shock grid and trained to lift their feet off the grid in the presence of a signal in order to avoid shock. Masker was a continuous tone. Signals were 20 msec tone bursts (5 msec rise/fall times, 2 bursts per sec) at 15 dB sensation level. Means: N=4.

The masker frequencies used were determined graphically from Fig. 4 in the reference with an accuracy of about 2%.

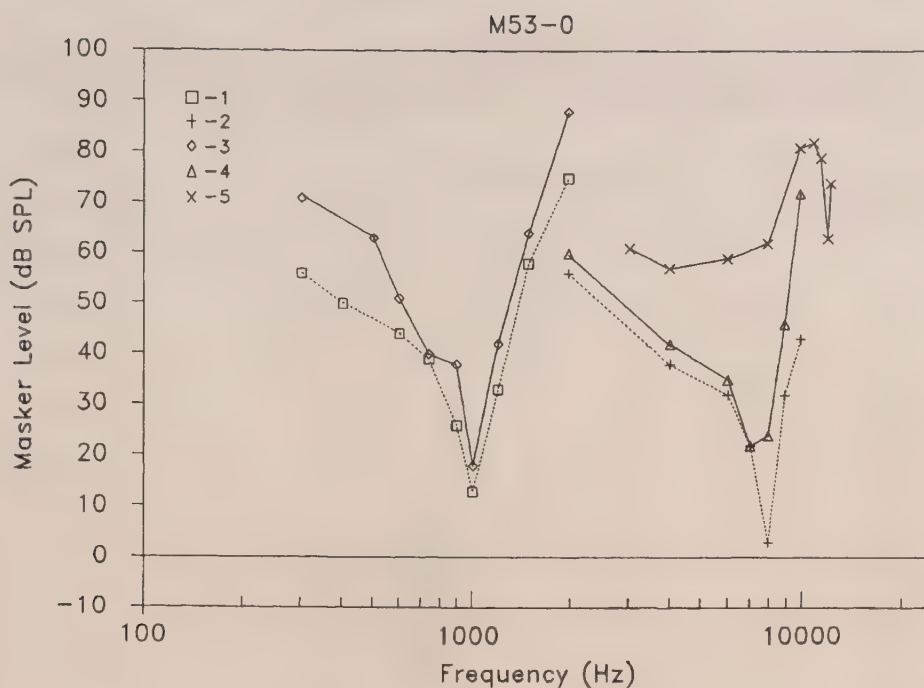


Fig. M53-0. Psychophysical tuning curves in *Chinchilla laniger* (chinchilla) before and following kanamycin administration (Ryan, Dallos, and McGee, 1979).

Before kanamycin treatment (Dashed lines)

1- 1000 Hz signal frequency

2- 8000 Hz

After kanamycin treatment (Solid lines)

3- 1000 Hz signal frequency

4- 8000 Hz

5- 11900 Hz

Reference:

Ryan, A., Dallos, P., and McGee, T. (1979) Psychophysical tuning curves and auditory thresholds after hair cell damage in the chinchilla. *J. Acoust. Soc. Amer.* 66, 370-378.

Table M53-0. Psychophysical tuning curves in *Chinchilla laniger* (chinchilla) before and following kanamycin administration (Ryan, Dallos, and McGee, 1979).

Masker Frequency (Hz)	Masker Level (dB SPL)				
	1	2	3	4	5
300	56		71		
400	50				
500			63		
600	44		51		
730	39		40		
900	26		38		
1000	13		18		
1200	33		42		
1500	58		64		
2000	75	56	88	60	
3000					61
4000		38		42	57
6000		32		35	59
7000		22		22	
8000		3		24	62
9000		32		46	
10000		43		72	81
11000					82
11350					79
11900					63
12200					74

Notes:

Instrumental shock avoidance (crossing a barrier) using the descending method of limits. Simultaneous masking. Masker was a continuous pure tone. The signal was a 38 msec pure tone with 10 msec rise/fall times, fixed at 10 dB sensation level. Kanamycin treatment was 200 mg/kg/day for 20 days. Testing was done 1-3 months after treatment. Hearing loss exceeded 40 dB at frequencies above 8000 Hz. Five functions were averaged for one animal (N=1).

Masker frequency values are probably accurate to within 2%.

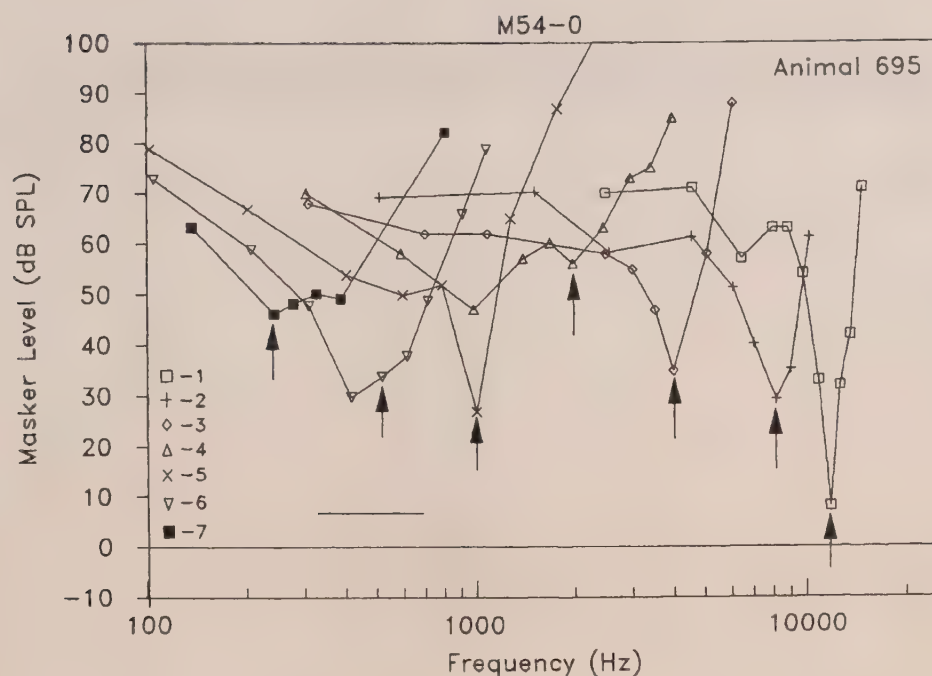


Fig. M54-0. Psychophysical tuning curves in *Chinchilla laniger* (chinchilla) following a 5-day exposure to a 500 Hz octave band of noise at 95 dB (Salvi, Perry, Hamernik, and Henderson, 1982). (Arrows indicate signal frequencies.)

- 1- 12000 Hz signal frequency
- 2- 8000 Hz
- 3- 4000 Hz
- 4- 2000 Hz
- 5- 1000 Hz
- 6- 500 Hz
- 7- 250 Hz

Line indicates the exposure noise bandwidth.

Reference:

Salvi, R., Perry, J., Hamernik, R.P., and Henderson, D. (1982) Relationships between cochlear pathologies and auditory nerve and behavioral responses following acoustic trauma. In R.P. Hamernik, D. Henderson, and R.J. Salvi (eds), *New Perspectives on Noise-Induced Hearing Loss*. Raven Press: New York, pp. 165-188.

Table M54-0. Psychophysical tuning curves in *Chinchilla laniger* (chinchilla) following a 5-day exposure to a 500 Hz octave band of noise at 95 dB (Salvi, Perry, Hamernik, and Henderson, 1982).

Masker Frequency (Hz)	Masker Level (dB SPL)						
	1	2	3	4	5	6	7
100					79	73	
140							63
200					67	59	
240							46
280							48
300			68	70		48	50
400					54	30	49
500		69				34	
600				58	50	38	
700			62			49	
800					52		82
900						66	
1000			62	47	27		
1050						79	
1300					65		
1400				57			
1500		70					
1700				60			
1800					87		
2000				56			
2400				63			
2500	70	58	58		104		
3000			55	73			
3400				75			
3500			47				
4000			35	85			
4500		61					
4600	71						
5000			58				
6000		51	88				
6400	57						
7000		40					
8000	63	29					
9000	63	35					
10000	54						
10200		61					
11000	33						
12000	3.5						
13000	31						
14000	41						
15000	70						

Notes:

Instrumental shock avoidance using tracking. Monaural animals. Simultaneous masking with continuous tone masker. 20 msec signal with 5 msec rise/fall times at 15 dB sensation level. 500 Hz octave band of noise at 95 dB for 5 days. N=1.

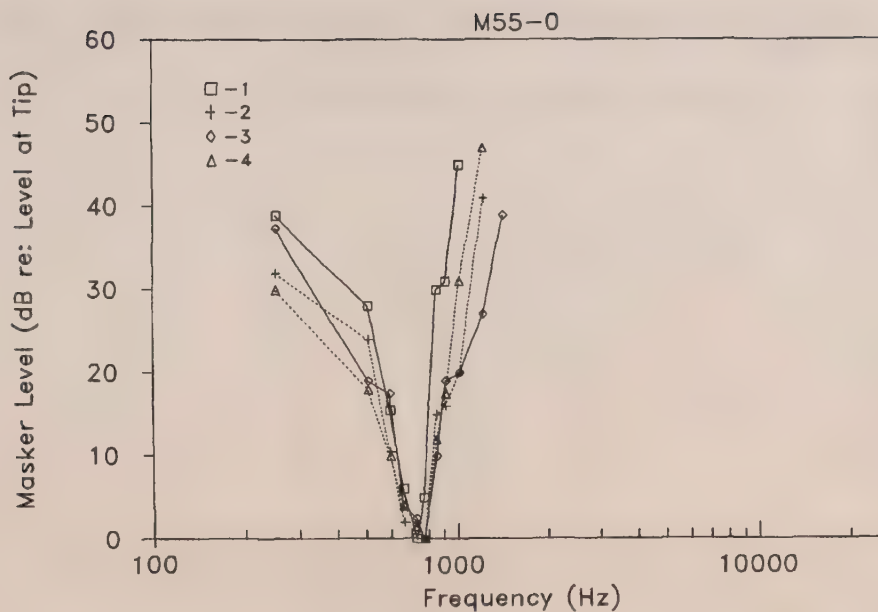


Fig. M55-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) (Clark and Bohne, 1986).

- 1- Animal 440R, before noise exposure
- 2- Animal 440R, after noise exposure
- 3- Animal 441R, before noise exposure
- 4- Animal 441R, after noise exposure

Reference:

Clark, W.W., and Bohne, B.A. (1986) Cochlear damage: Audiometric correlates. In M.J. Collins, T.J. Glatke, and L.A. Harker (eds), *Sensorineural Hearing Loss: Mechanisms, Diagnosis, and Treatment*. University of Iowa Press: Iowa City.

Table M55-0. Psychophysical tuning curves for *Chinchilla laniger* (chinchilla) (Clark and Bohne, 1986).

Masker Frequency (Hz)	Masker Level (dB re: Level at Tip Frequency)			
	1	2	3	4
250	39	32	37.5	30
500	28	24	19	18
590	15.5	10.5	17.5	10
650	6	2	4	4
715	0	2	2.5	1.5
760	5	0	0	0
840	30	15	10	12
900	31	16	19	17.5
1000	45	20	20	31
1200		41	27	47
1400			39	

Notes:

Operant conditioning for a food reward using a tracking psychophysical procedure. The animal was trained to depress an observing lever and hold it for a variable period (1-6 sec). If the animal released the lever during the 2-sec tone trial, it was reinforced with food. Left ear destroyed. 10 msec rise/fall times. Continuous tonal masker in simultaneous masking. Signal fixed at 715 Hz, 20 dB sensation level. Noise exposure consisted of 500 Hz octave band at 95 dB SPL for 36 days. There is no consistent effect of the noise exposure on these psychophysical tuning curves. N=2.

These data are from a book chapter in which other audiometric data (normal and following noise exposure) are reported for the same individual.

See Fig. M59-0 for Q_{10dB} values.

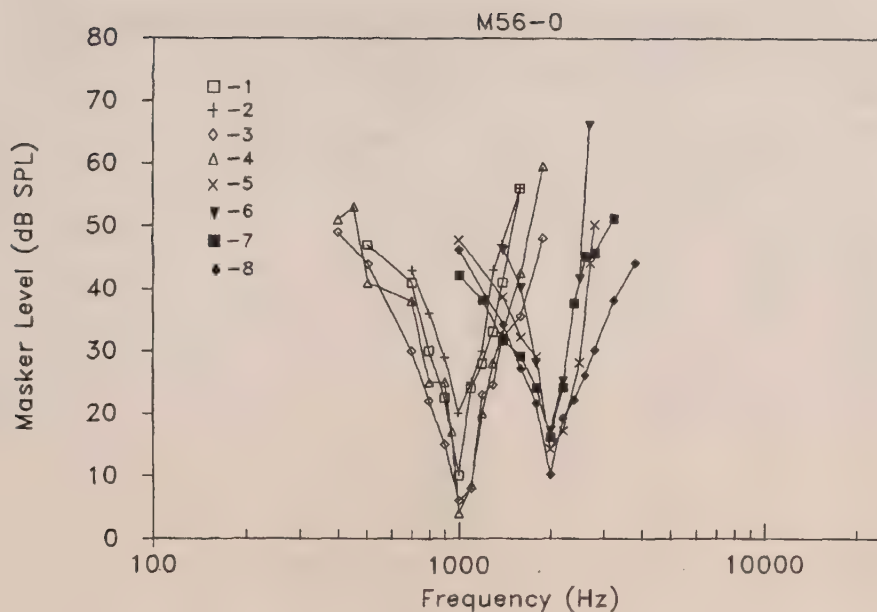


Fig. M56-0. Psychophysical tuning curves for *Felis catus* (cat) (Pickles, 1979).

1-4- Four animals tested with 1000 Hz signal frequency
 5-8- Four animals tested with 2000 Hz signal frequency

Reference:

Pickles, J.O. (1979) Psychophysical frequency resolution in the cat as determined by simultaneous masking and its relation to auditory nerve resolution. *J. Acoust. Soc. Amer.* 66, 1725-1732.

Table M56-0. Psychophysical tuning curves for *Felis catus* (cat) (Pickles, 1979).

Masker Frequency (Hz)	Masker Level (dB SPL)							
	1	2	3	4	5	6	7	8
400			49	51				
450				53				
500	47		44	41				
700	41	43	30	38				
800	30	36	22	25				
900	22.5	29	15	25				
950				17				
1000	10	20	6	4	47.5		42	46
1100	24	25	8	8.5				
1200	28	30	23	20			38	
1300	33	43	24.5	28				
1400	41	47	32	32.5	38.5	46	31.5	34
1600	56	56	35.5	42.5	32	40	29	27
1800					29	28	24	21.5
1900			48	59.5				
2000					14	17	16	10
2200					17	25	24	19
2400							37.5	22
2500					28	41.5		
2600							45	26
2700					44	66		
2800					50		45.5	30
3250							51	38
3800								44

Notes:

Instrumental shock avoidance (tilt cage) using a tracking procedure. Signals were 150 msec tone bursts with 22 msec rise/fall times presented at 10 dB sensation level. Masker was continuous tone (simultaneous masking). When the signal and masker frequency were equal, the signal was added at 90° phase angle to the masker. Individual animal data are shown.

See Fig. M59-0 for Q_{10dB} values for these data.

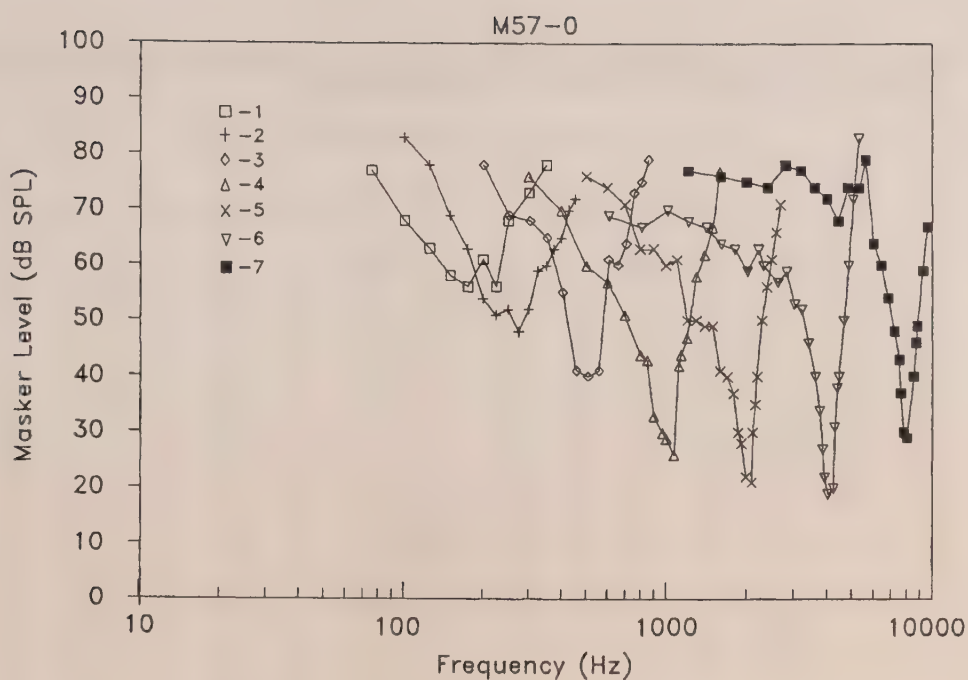


Fig. M57-0. Psychophysical tuning curves for *Macaca nemestrina* (pig-tailed macaque) in simultaneous masking (Serafin, Moody, and Stebbins, 1982).

- 1- 125 Hz signal frequency
- 2- 250 Hz
- 3- 500 Hz
- 4- 1000 Hz
- 5- 2000 Hz
- 6- 4000 Hz
- 7- 8000 Hz

Reference:

Serafin, S.V., Moody, D.B., and Stebbins, W.C. (1982) Frequency selectivity of the monkey's auditory system: Psychophysical tuning curves. *J. Acoust. Soc. Amer.* 71, 1513-1518.

Table M57-0. Psychophysical tuning curves for *Macaca nemestrina* (pig-tailed macaque) in simultaneous masking (Serafin, Moody, and Stebbins, 1982).

Masker Frequency in Hz, Masker Level in dB SPL													
Hz	1 dB	Hz	2 dB	Hz	3 dB	Hz	4 dB	Hz	5 dB	Hz	6 dB	Hz	7 dB
75	77	100	83	200	78	300	76	500	76	600	69	1200	77
100	68	125	78	250	69	400	70	600	74	800	67	1600	76
125	63	150	69	300	68	500	60	700	71	1000	70	2000	75
150	58	175	63	350	65	600	57	800	63	1200	68	2400	74
175	56	150	69	400	55	700	51	900	63	1400	67	2800	78
200	61	175	63	450	41	800	44	1000	60	1600	64	3200	77
225	56	200	54	500	40	850	43	1100	61	1800	63	3600	74
250	68	225	51	550	41	900	33	1200	50	2000	59	4000	72
300	73	250	52	600	61	970	30	1300	50	2200	63	4400	68
350	78	275	48	650	60	1000	28	1400	49	2300	60	4800	74
		300	52	700	64	1070	26	1500	49	2600	57	5300	74
		325	59	750	73	1120	42	1600	41	2800	59	5600	79
		350	60	800	75	1140	44	1700	40	3000	53	6000	64
		375	63	850	79	1200	47	1800	37	3200	52	6400	60
		400	65			1300	58	1875	30	3400	46	6800	54
		425	70			1400	62	1920	28	3600	40	7200	48
		450	72			1500	67	2000	22	3740	34	7500	43
						1600	77	2100	21	3830	27	7600	37
								2120	30	3900	22	7800	30
								2170	35	4000	19	8000	29
								2200	40	4200	20	8500	40
								2300	50	4250	31	8700	46
								2400	56	4350	38	8800	49
								2500	61	4400	40	9200	59
								2600	56	4600	50	9600	67
								2700	71	4800	60		
										5000	72		
										5240	82		

Notes:

Operant conditioning for a food reward using a tracking procedure. Animals were trained to contact a manipulandum as an observing response, and to release after signal onset for a reward. The masker tone was continuous. The signal was a 2.5 sec tone burst with 50 msec rise/fall times, delivered through earphones at 10 dB sensation level. Data shown are for one animal (M-102). Each point is the median of five threshold estimates.

See Fig. M59-0 for Q_{10dB} values determined in this study. See Fig. M58-0 for forward masking tuning curves.

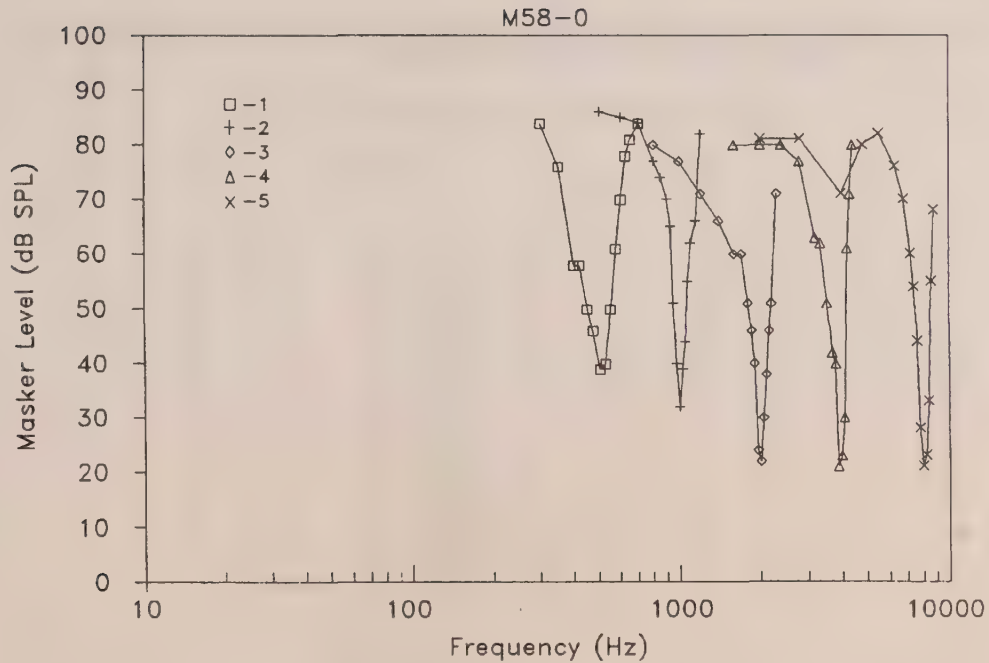


Fig. M58-0. Psychophysical tuning curves for *Macaca nemestrina* (pig-tailed macaque) in forward masking (Serafin, Moody, and Stebbins, 1982).

- 1- 500 Hz signal frequency
- 2- 1000 Hz
- 3- 2000 Hz
- 4- 4000 Hz
- 5- 8000 Hz

Reference:

Serafin, S.V., Moody, D.B., and Stebbins, W.C. (1982) Frequency selectivity of the monkey's auditory system: Psychophysical tuning curves. *J. Acoust. Soc. Amer.* 71, 1513-1518.

Table M58-0. Psychophysical tuning curves for *Macaca nemestrina* (pig-tailed macaque) in forward masking (Serafin, Moody, and Stebbins, 1982).

Masker Frequency in Hz, Masker Level in dB SPL									
Hz	1 dB	Hz	2 dB	Hz	3 dB	Hz	4 dB	Hz	5 dB
300	84	500	86	800	80	1600	80	2000	81
350	76	600	85	1000	77	2000	80	2800	81
400	58	700	84	1200	71	2400	80	4000	71
420	58	800	77	1400	66	2800	77	4800	80
470	46	850	74	1600	60	3200	63	5500	82
500	39	900	70	1700	60	3350	62	6300	76
525	40	940	65	1800	51	3550	51	6800	70
550	50	950	51	1850	46	3700	42	7200	60
575	61	970	40	1900	40	3800	40	7400	54
600	70	1000	32	1950	24	3900	21	7600	44
625	78	1015	39	2000	22	4000	23	7800	28
650	81	1050	44	2050	30	4100	30	8000	21
700	84	1080	55	2100	38	4200	61	8200	23
		1100	62	2150	46	4300	71	8400	33
		1150	66	2200	51	4400	80	8600	55
		1200	82	2300	71			8800	68

Notes:

Operant conditioning for a food reward using a tracking procedure. Animals were trained to contact a manipulandum as an observing response, and to release after signal onset for a reward. The masker tone was pulsed for 130 msec (10 msec rise/fall times). The signal was a 25 msec tone burst with 10 msec rise/fall times, delivered through earphones at 10 dB sensation level. The signal rise began 2 msec after masker fell to zero (at masker offset). Data shown are for one animal (M-117). Each point is the median of five thresholds estimates.

See Fig. M59-0 for Q_{10dB} values determined in this study. See Fig. M57-0 for simultaneous masking tuning curves.

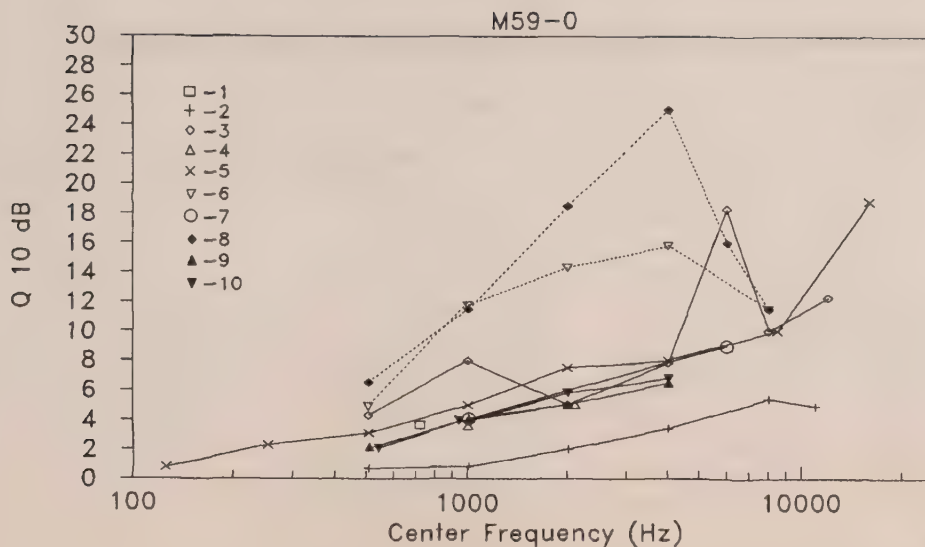


Fig. M59-0. Q_{10dB} of psychophysical tuning curves from several mammals.

- 1- *Chinchilla laniger* - chinchilla (Clark and Bohne, 1986)
- 2- *Chinchilla laniger* - chinchilla (Salvi, Ahroon, Perry, Gunnarson, and Henderson, 1982)
- 3- *Chinchilla laniger* - chinchilla (McGee, Ryan, and Dallos, 1976)
- 4- *Felis catus* - cat (Pickles, 1979)
- 5-6- *Macaca nemestrina* - pig-tailed macaque (Serafin, Moody, and Stebbins, 1982)
5- simultaneous masking, 6- forward masking
- 7- *Homo sapiens* - human (simultaneous masking) (Moore, 1978)
- 8- *Homo sapiens* - human (forward masking) (Moore, 1978)
- 9- *Homo sapiens* - human adult (Olsho, 1985)
- 10- *Homo sapiens* - human infants, 5-8 months old (Olsho, 1985)

References:

- Clark, W.W., and Bohne, B.A. (1986) Cochlear damage: Audiometric correlates. In M.J. Collins, T. Glatke, and L.A. Harker (eds), *Sensorineural Hearing Loss: Mechanisms, Diagnosis, and Treatment*. University of Iowa Press: Iowa City.
- Olsho, L.W. (1982) Infant auditory perception: Tonal masking. *Infant Behav. and Develop.* 8, 371-384.
- McGee, T., Ryan, A., and Dallos, P. (1976) Psychophysical tuning curves of chinchillas. *J. Acoust. Soc. Amer.* 60, 1146-1150.
- Moore, B.C.J. (1978) Psychophysical tuning curves measured in simultaneous and forward masking. *J. Acoust. Soc. Amer.* 63, 524-532.
- Pickles, J.O. (1979) Psychophysical frequency resolution in the cat as determined by simultaneous masking and its relation to auditory nerve resolution. *J. Acoust. Soc. Amer.* 66, 1725-1732.
- Salvi, R.J., Ahroon, W.A., Perry, J.W., Gunnarson, A.D., and Henderson, D. (1982) Comparison of psychophysical and evoked-potential tuning curves in the chinchilla. *Am. J. Otolaryngol.* 3, 408-416.

Table M59-0. Q_{10dB} of psychophysical tuning curves from several mammals.

Center Frequency (Hz)	Q_{10dB}									
	1	2	3	4	5	6	7	8	9	10
125					0.8					
250					2.3					
500		0.7	4.3		3.1	4.9		6.5	2.2	2.1
715	3.7									
1000		0.85	8	4	5	11.8	4.1	11.5	4.1	4
2000		2	5	5	7.5	14.3		18.5	5	5.8
4000		3.4	7.8		8	15.8		25	6.5	6.8
6000			18.3				9	16		
8000		5.4	10		10	11.5		11.5		
11000		4.9								
12000			12.3							
16000						18.8				

Notes:

Dashed lines indicate forward masking conditions.

Q_{10dB} is a relative measure of the sharpness of tuning (selectivity) of a filter. It is defined as the center frequency of the filter divided by the bandwidth 10 dB above the sensitivity at the center frequency. Large values indicate sharp tuning.

1- See Notes for Fig. M55-0. Data derived from psychophysical tuning curves (PTC) determined for two animals using simultaneous masking.

2- See Notes for Fig. M51-0. Simultaneous masking. Medians: N=4.

3- See Notes for Fig. M50-0. Points connect the median Q_{10dB} values of PTCs obtained at the indicated signal frequencies. Data for simultaneous, forward, and "partial" forward masking combined since no significant differences resulted from using these different methods. The points at 1 kHz and 8 kHz are based on 30 individual PTCs. N=1 to 3 at the other signal frequencies.

4- See Notes for Fig. M56-0. Data are from four PTCs obtained at each center frequency using simultaneous masking.

5- See Notes for Fig. M57-0. Simultaneous masking. Medians: N=1 at 125 Hz, N=2 at 250 Hz and 16 kHz, and N=3 for all other frequencies.

6- See Notes for Fig. M58-0. Forward Masking. Medians: N=3

7- See Notes for Fig. M60-0. Simultaneous masking. Means: N=3.

8- See Notes for Fig. M60-0. Forward masking. Means: N=3.

9- See Notes for Fig. M61-0. Simultaneous masking. Means: N=6 adults

10- See Notes for Fig. M61-0. Simultaneous masking. Means: N=6 infants

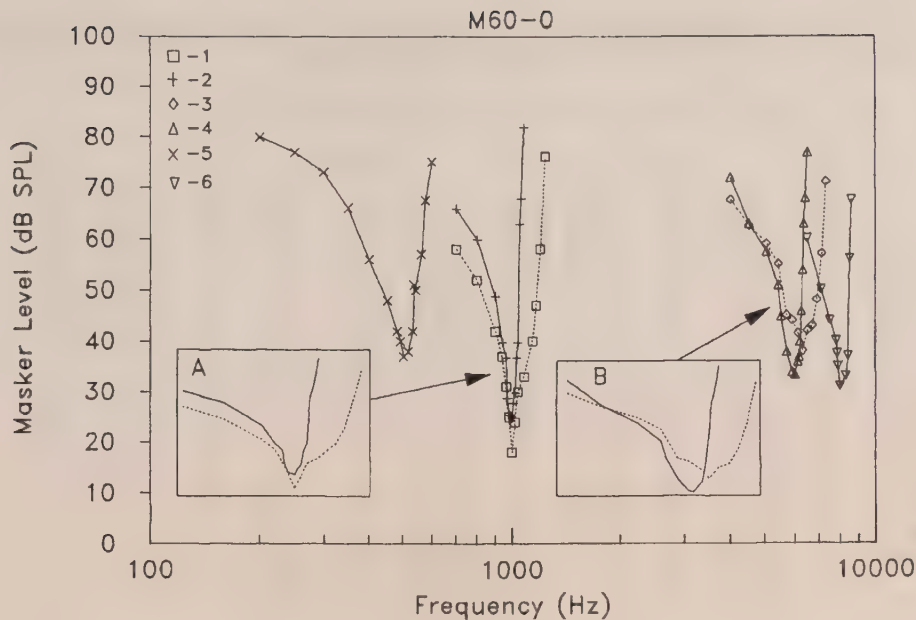


Fig. M60-0. Psychophysical tuning curves in *Homo sapiens* (human) in simultaneous (dashed lines) and forward (solid lines) masking (Moore, 1978).

- 1- Simultaneous masking, 1000 Hz signal frequency
- 2- Forward masking, 1000 Hz signal frequency
- 3- Simultaneous masking, 6000 Hz signal frequency
- 4- Forward masking, 6000 Hz signal frequency
- 5- Forward masking, 500 Hz signal frequency
- 6- Forward masking, 8000 Hz signal frequency

A Inset- 1 & 2 expanded without symbols
 B Inset- 3 & 4 expanded without symbols

Reference:

Moore, B.C.J. (1978) Psychophysical tuning curves measured in simultaneous and forward masking. *J. Acoust. Soc. Amer.* 63, 524-532.

Table M60-0. Psychophysical tuning curves in *Homo sapiens* (human) in simultaneous (dashed lines) and forward (solid lines) masking (Moore, 1978).

Masker Frequency in Hz, Masker Level in dB											
1		2		3		4		5		6	
Hz	dB	Hz	dB	Hz	dB	Hz	dB	Hz	dB	Hz	dB
700	58	700	66	4000	67.5	4000	72	200	80	6500	60
800	52	800	60	4500	62.5	4500	63	250	77	7100	50
900	42	900	49	5000	59	5000	57.5	300	73	7500	44
940	37	940	40	5400	55	5400	51	350	66	7800	40
960	31	960	37	5700	45	5500	45	400	56	7850	37.5
980	25	970	29	5900	44	5700	38	450	48	7900	35
1000	18	980	26	6100	41.5	5900	34	480	42	8000	31
1020	24	990	25.5	6300	38	6000	33.5	490	40	8300	33
1040	30	1000	25	6500	42	6100	36	500	37	8400	37
1080	33	1010	28	6700	43	6160	37	515	38	8500	56
1140	40	1020	30	6900	48	6200	40	530	42	8600	67.5
1170	47	1030	37	7100	57	6250	46	535	51		
1200	58	1040	40	7300	71	6300	54	540	50		
1240	76	1050	63			6340	63	560	57		
		1060	68			6400	68	575	67.5		
		1080	82			6500	77	600	75		

Notes:

Frequencies are best estimates from a graphical presentation with an error no larger than 1%.

Two-interval, forced-choice task using a tracking procedure.

The insets show the simultaneous (dashed line) and forward (solid line) masking tuning curves expanded and without symbols in order to better illustrate the differences resulting from the two masking paradigms. See Fig. M59-0 for Q_{10dB} values from this study.

2 & 4- Simultaneous masking. Tone masker was 300 msec burst with 17 msec rise/fall times. The signal (10 dB sensation level) was 34 msec in duration (17 msec rise fall times), reaching peak amplitude coincident with the start of the "fall" of the masker. Data are for one subject (BM).

1 & 3- Forward masking. The masker was the same as above. The signal "rise" began at the same time that the masker "fall" reached zero. Data are for one subject (BM).

5 & 6- Forward masking for another subject (PMP).

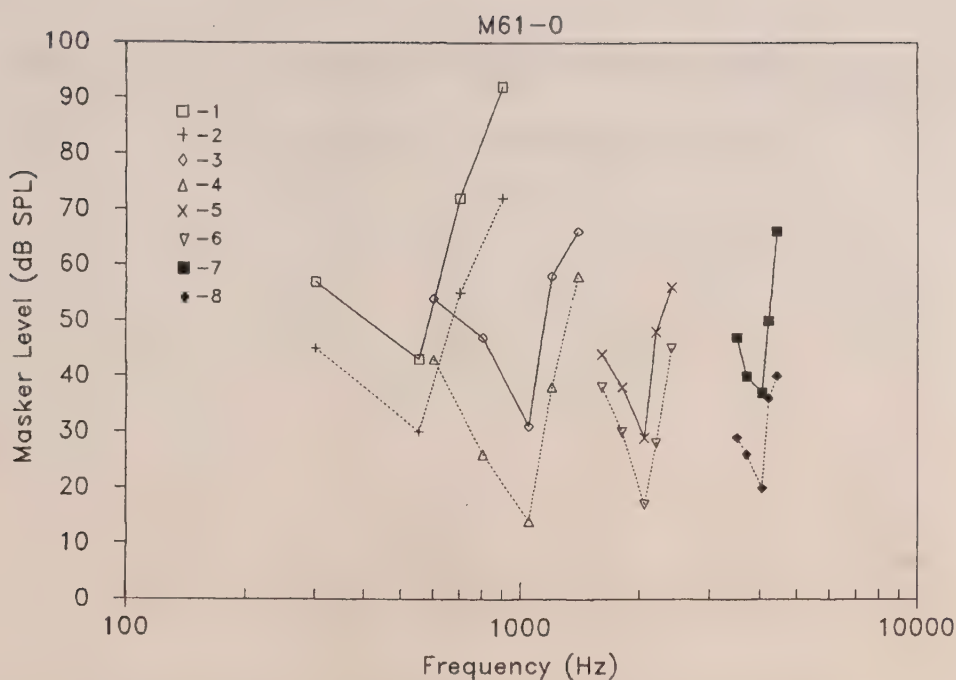


Fig. M61-0. Psychophysical tuning curves in *Homo sapiens* (human), adults and infants (Olsho, 1985).

1- Adult, 500 Hz signal frequency
2- Infant, 500 Hz

3- Adult, 1000 Hz
4- Infant, 1000 Hz

5- Adult, 2000 Hz
6- Infant, 2000 Hz

7- Adult, 4000 Hz
8- Infant, 4000 Hz

Solid lines: Adult
Dashed lines: Infants

Reference:

Olsho, L.W. (1985) Infant auditory perception: Tonal masking. *Infant Behav. and Develop.* 8, 371-384.

Table M61-0. Psychophysical tuning curves in *Homo sapiens* (human), adults and infants (Olsho, 1985).

Masker Frequency in Hz, Masker Level in dB SPL					
	1	2		3	4
Hz	dB	dB	Hz	dB	dB
300	57	45	1600	44	38
550	43	30	1800	38	30
700	72	55	2050	29	17
900	92	72	2200	48	28
			2400	56	45
	5	6		7	8
Hz	dB	dB	Hz	dB	dB
600	54	43			
800	47	26	3500	47	29
1050	31	14	3700	40	26
1200	58	38	4050	37	20
1400	66	58	4200	50	36
			4400	66	40

Notes:

Visually reinforced head-turn procedure using the "two-down, one-up" rule in a tracking method. In the presence of the signal, infants turning their head toward a mechanical toy were reinforced by the activation of the toy. A "blind" observer decided when a head-turn occurred. Simultaneous masking. Maskers were six sec pure tone bursts with 10 msec rise/fall times. Signals were 100 msec tone bursts with 10 msec rise/fall times presented through headphones at 25 dB sensation level.

Each threshold point based on data averaged across subjects, some of which may not have been tested at all masker frequencies. Six infants and six adults were tested at each signal frequency. A total of 24, 4-8 month-old infants and 24 adults were subjects.

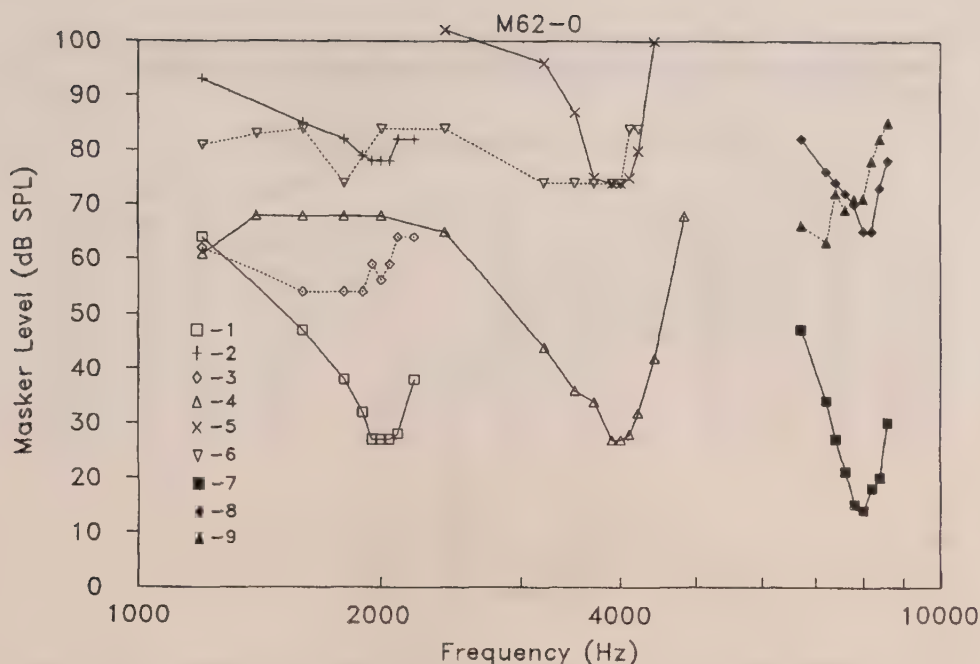


Fig. M62-0. Psychophysical tuning curves for *Erythrocebus patas* (patas monkey) determined at different signal levels and following dihydrostreptomycin-sulfate ototoxicity.

- 1- Signal frequency 2000 Hz, signal level 10 dB SL (normal)
- 2- Signal frequency 2000 Hz, signal level 60 dB SL (normal)
- 3- Signal frequency 2000 Hz, signal level 10 dB SL (60 days post drug)
- 4- Signal frequency 4000 Hz, signal level 10 dB SL (normal)
- 5- Signal frequency 4000 Hz, signal level 60 dB SL (normal)
- 6- Signal frequency 4000 Hz, signal level 10 dB SL (41 days post drug)
- 7- Signal frequency 8000 Hz, signal level 10 dB SL (normal)
- 8- Signal frequency 8000 Hz, signal level 60 dB SL (normal)
- 9- Signal frequency 8000 Hz, signal level 10 dB SL (23 days post drug)

Ototoxicity data from Smith, Moody, Stebbins, and Norat (1987) and normal data from Smith, Moody and Stebbins (1987).

References:

- Smith, D.W., Moody, D.B., and Stebbins, W.C. (1987) The effects of changes in absolute measurement level on psychophysical tuning curves in quiet and noise in patas monkeys. *J. Acoust. Soc. Amer.* 82, 63-68.
- Smith, D.W., Moody, D.B., Stebbins, W.C., and Norat, M.A. (1987) Effects of outer hair cell loss on the frequency selectivity of the patas monkey auditory system. *Hear. Res.* 29, 125-138.

Table M62-0. Psychophysical tuning curves for *Erythrocebus patas* (patas monkey) determined at different signal levels and following dihydrostreptomycin-sulfate ototoxicity.

Masker Frequency in Hz, Masker Level in dB SPL											
Hz	dB			Hz	dB			Hz	dB		
	1	2	3		4	5	6		7	8	9
1200	64	93	62	1200	61		81	6700	47	82	66
1600	47	85	54	1400	68		83	7200	34	76	63
1800	38	82	54	1600	68		84	7400	27	74	72
1900	32	79	54	1800	68		74	7600	21	72	69
1950	27	78	59	2000	68		84	7800	15	70	71
2000	27	78	56	2400	65	102	84	8000	14	65	71
2050	27	78	59	3200	44	96	74	8200	18	65	78
2100	28	82	64	3500	36	87	74	8400	20	73	82
2200	38	82	64	3700	34	75	74	8600	30	78	85
				3900	27	74	74				
				4000	27	74	74				
				4100	28	75	84				
				4200	32	80	84				
				4400	42	100					
				4800	68						

Notes:

Operant conditioning for a food reward using a tracking procedure. Animals were trained to contact a manipulandum (observing response) and to release it in the presence of a signal. Forward masking. Masker was 130 msec tone bursts (5 msec rise/fall times), separated by 130 msec of silence. Signal was a 25 msec tone burst (5 msec rise/fall times) presented after masker offset so that 10 msec separated the time of masker fall to 50% and the time of signal rise to 50%.

3-, 6-, 9- Dihydrostreptomycin-sulfate administered daily at a dose of 20 mg/kg/day until a threshold shift of 10 dB was observed at 16 kHz.

All data are from individual animals. #4-#9 from animal M-155, #1-#3 from animal M-157.

The normal thresholds for #4 and #6 at frequencies below 2400 Hz were taken from the "baseline" data from Smith, Moody, Stebbins, and Norat (1987) which these authors attributed to Smith, Moody, and Stebbins (1987).

The authors point out that the effect of the ototoxic drug is to detune the psychophysical tuning curves more than would have occurred simply by raising signal level to maintain a constant sensation level.

These references contain many more psychophysical tuning curves for other animals, other conditions, and other times following drug administration. Smith, Moody, and Stebbins (1987) includes psychophysical tuning curves determined in the presence of various levels of broad band masking noise. The noise tends to detune the tuning curves. In humans, noise elevates the tuning curves but tends not to detune them when they are compared at equal signal SPL.

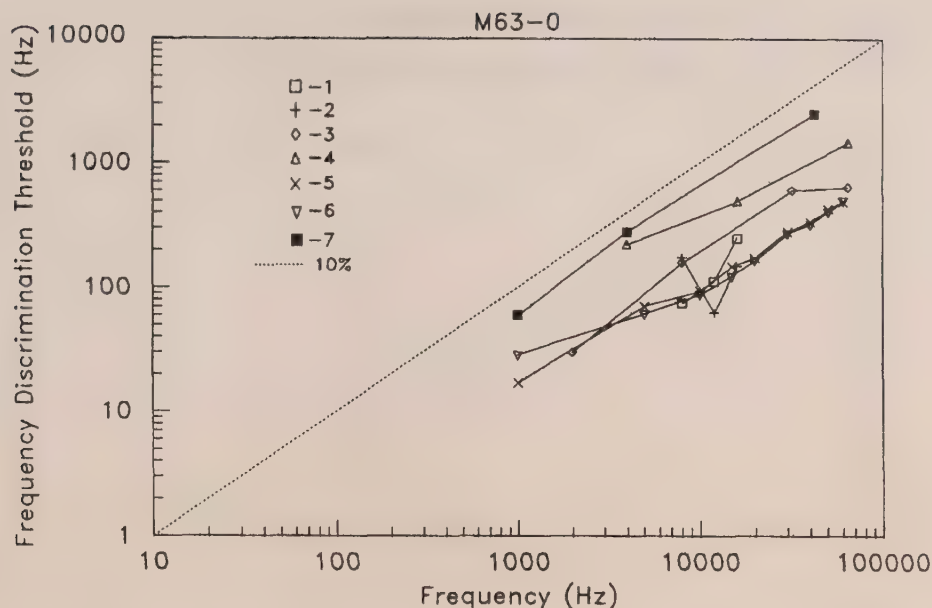


Fig. M63-0. Frequency discrimination thresholds in some rodents.

- 1- *Mus musculus* - laboratory mouse (C57BL/6) (Kulig and Willott, 1984)
- 2- *Mus musculus* - laboratory mouse (DBA/2) (Kulig and Willott, 1984)
- 3- *Sigmodon hispidus* - cotton rat (Heffner and Masterton, 1980)
- 4- *Mus musculus* - feral house mouse (Heffner and Masterton, 1980)
- 5- *Mus musculus* - laboratory mouse (tone bursts) (Ehret, 1975b)
- 6- *Mus musculus* - laboratory mouse (sinusoidal FM) (Ehret, 1975b)
- 7- *Rattus norvegicus* - albino rat (Kelly, 1970)

References:

- Ehret, G. (1975b) Frequency and intensity difference limens and nonlinearities in the ear of the housemouse (*Mus musculus*). *J. Comp. Physiol.* 102, 321-336.
- Heffner, H., and Masterton, R. (1980) Hearing in glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *J. Acoust. Soc. Amer.* 68, 1584-1599.
- Kelly, J.B. (1970) The effects of lateral lemniscal and neocortical lesions on auditory absolute thresholds and frequency difference thresholds in the rat. Ph.D. Thesis, Vanderbilt University, University Microfilms 70-16, 429.
- Kulig, J., and Willott, J.F. (1984) Frequency difference limens of C57BL/6 and DBA/2 mice: Relationship between auditory neuronal response properties and hearing impairment. *Hear. Res.* 16, 169-174.

Table M63-0. Frequency discrimination thresholds in some rodents.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)						
	1	2	3	4	5	6	7
1000					17	28	60
2000			30				
4000				224			280
5000					70	60	
8000	75	175	160				
10000					95	87	
12000	113	63					
15000					150	122	
16000	250	150		496			
20000					174	164	
30000					285	270	
32000			608				
40000					340	320	
42000							2520
50000						430	405
60000						492	492
64000			640	1472			

Notes:

1- Instrumental shock avoidance (jumping to "safe" platform) using the method of constant stimuli. Signals were 40 dB sensation level alternating 800 msec and 200 msec tone bursts with 5 msec rise/fall times. The 15 sec conditioned stimulus was an alternation of the frequency of the 200 msec burst. Animals 4 weeks old. Means: N=6.

2- Same as #1. Means: N=5.

3- Classically conditioned suppression of licking using a tracking procedure and the method of constant stimuli. Animals were trained to lick a drinking spout for a water reward. Tone presentations signalled impending shock, and suppressed the operant licking behavior. Signals were 30 dB sensation level bursts, 700 msec "on" and 300 msec "off." The conditioned stimulus was an alternation in frequency of successive bursts for 10 sec. Means: N=3.

4- Same as #3.

5- Operant conditioning for a water reward using the method of constant stimuli. Animals learned to approach and lick a drinking tube during frequency increments. Signals were 100 msec tone bursts (10 msec rise/fall times) repeated 5 times per sec. The conditioned stimulus was an alternation of the frequency of successive bursts. The thresholds plotted here are at 40 dB sensation level. Data were collected at a wide range of sensation levels (see Fig. M69-0). Means: N=7.

6- Same as #5 except that the conditioned stimulus was a 4.5 Hz sinusoidal frequency modulation impressed upon a background tone.

7- Classically conditioned suppression of operant behavior using the method of constant stimuli. Signals were 900 msec tone bursts at 30 dB sensation level. The conditioned stimulus was an alternation of the frequency of successive bursts. Means: N=2.

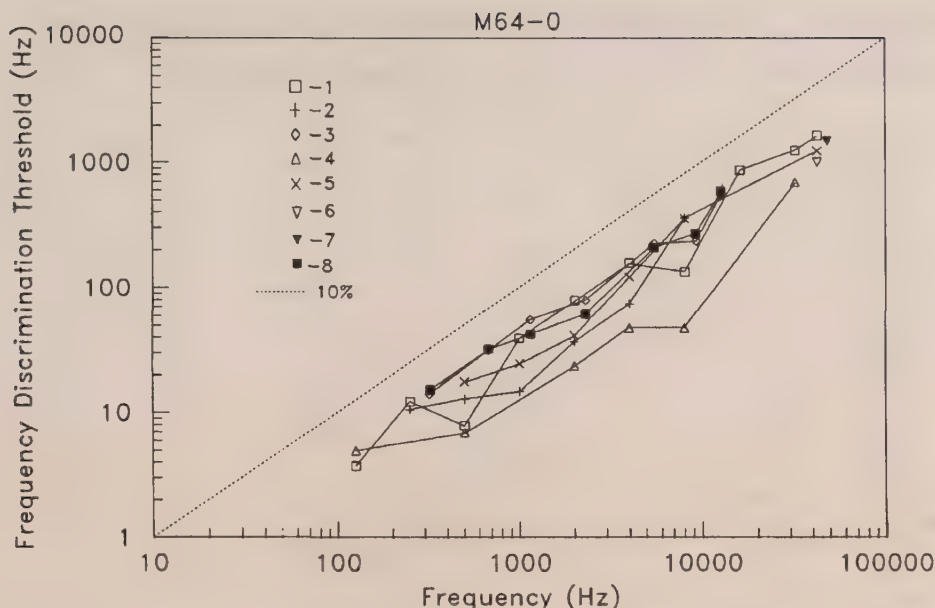


Fig. M64-0. Frequency Discrimination thresholds for several mammal species.

- 1- *Cavia procellus* - guinea pig (Heffner, Heffner, and Masterton, 1971)
- 2- *Chinchilla laniger* - chinchilla (Nelson and Kiester, 1978)
- 3- *Chinchilla laniger* - chinchilla (Long and Clark, 1984)
- 4- *Galago senegalensis* - bushbaby (Heffner, Ravizza, and Masterton, 1969b)
- 5- *Tupaia glis* - tree shrew (Heffner, Ravizza, and Masterton, 1969a)
- 6- *Hemiechinus auritus* - hedgehog (Ravizza, Heffner, and Masterton, 1969b)
- 7- *Didelphis virginianus* - opossum (Ravizza, Heffner, and Masterton, 1969a)
- 8- *Chinchilla laniger* - chinchilla (Clark and Bohne, 1986)

References:

- Heffner, R., Heffner, H., and Masterton, R.B. (1971) Behavioral measurement of absolute and frequency-difference thresholds in guinea pig. *J. Acoust. Soc. Amer.* 49, 1888-1895.
- Heffner, H.E., Ravizza, R.J. and Masterton, B. (1969a) Hearing in primitive mammals: III Tree shrew (*Tupaia glis*). *J. Aud. Res.* 9, 12-18.
- Heffner, H., Ravizza, R.J., and Masterton, B. (1969b) Hearing in Primitive mammals IV: Bushbaby (*Galago senegalensis*). *J. Aud. Res.* 9-19-23.
- Long, G., and Clark, W. (1984) Detection of frequency and rate modulation by the chinchilla. *J. Acoust. Soc. Amer.*, 1984, 75, 1184-1190.
- Nelson, D. A., and Kiester, T. E. (1978) Frequency discrimination in the chinchilla. *J. Acoust. Soc. Amer.* 64, 114-126.
- Ravizza, R., Heffner, H., and Masterton, B. (1969a) Hearing in primitive mammals I: Opossum (*Didelphis virginianus*). *J. Aud. Res.* 9, 1-7.
- Ravizza, R., Heffner, H., and Masterton, B. (1969b) Hearing in primitive mammals II: Hedgehog (*Hemiechinus auritus*). *J. Aud. Res.* 9, 8-11.
- Clark, W.W., and Bohne, B.A. (1986) Cochlear damage: Audiometric correlates. In M.J. Collins, T.J. Glatke, and L.A. Harker (eds), *Sensorineural Hearing Loss: Mechanisms, Diagnosis, and Treatment*. University of Iowa Press: Iowa City.

Table M64-0. Frequency Discrimination thresholds for several mammal species.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)							
	1	2	3	4	5	6	7	8
125	3.8			5				
250	12.5	10.7						
320			14.2					15.8
500	8	13		7	18			
675			31.8					33
1000	40	15			25			
1150			56.1					43
2000	80	37.3		24	42			
2300			79.7					62
4000	160	74.5		48	124			
5500			227.5					209
8000	136	362		48	360			
9250			238					268
12750			566.9					574
16000	880							
32000	1280			704				
42000	1680				1260	1000	1512	

Notes:

1- Classically conditioned suppression of an operant response using the method of limits and the method of constant stimuli. Animals were trained to lick a water spout for a water reward on an intermittent reinforcement schedule. Tone presentations signalled impending foot shock and suppressed licking. Signals were 700 msec tone bursts at 30 dB sensation level. Signals above 500 Hz had 25 msec rise/fall times. Signals below 500 Hz had longer rise/fall times. The conditioned stimulus was an alternation of the frequency of adjacent bursts for 10 sec. Means: N=2.

2- Instrumental shock avoidance in a double grill box using an adaptive tracking procedure. Signals were 250 msec tone bursts (25 msec rise/fall times) at 54-73 dB sensation level. Conditioned stimulus was an alternation of the frequency of successive ongoing background tone bursts. Means: N=6.

3- Operant conditioning for a food reward using an adaptive tracking procedure. Animals were trained to press a lever to initiate a trial, and then to release the lever only during a signal. The signal consisted of a 2 Hz sinusoidal frequency modulation impressed on a continuous carrier at 40 dB sensation level (SL). Thresholds expressed in terms of root mean square (RMS) amplitude of frequency modulation. (Data were also obtained at 20 and 60 dB SL but were not plotted here. There is a small tendency for the frequency discrimination threshold to be lower at the higher SLs). Means: N=3.

4- Classically conditioned suppression of an operant response (licking a spout for food) using the method of constant stimuli. Signals were repeating 700 msec tone bursts and the conditioned stimulus was an alternation of the frequency of successive bursts. Means: N=2.

5- Same as #4. Means: N=2.

6- Same as #4. Means: N=2.

7- Same as #4. Means: N=2.

8- Same as #3. 40 dB sensation level. N=1.

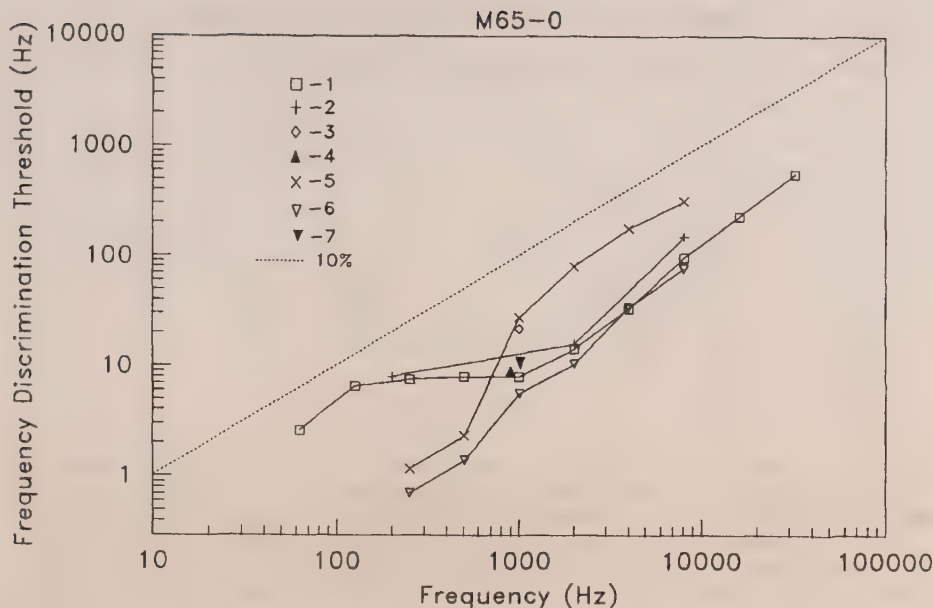


Fig. M65-0. Frequency discrimination in several mammal species.

- 1- *Felis catus* - cat (Elliott, Stein, and Harrison, 1960)
- 2- *Felis catus* - cat (Butler, Diamond, and Neff, 1957)
- 3- *Canis canis* - dog (absolute memory) (Baru, 1971)
- 4- *Canis canis* - dog (relative) (Baru, 1971)
- 5- *Elephas maximus* - elephant (75% criterion) (Heffner and Heffner, 1982)
- 6- *Elephas maximus* - elephant (statistical criterion) (Heffner and Heffner, 1982)
- 7- *Felis catus* - cat (Thompson, 1960)

References:

- Baru, A.V. (1971) Behavioral thresholds and frequency difference limen as a function of sound duration in dogs deprived of the auditory cortex. In G.V. Gersuni (ed), *Sensory Processes at the Neuronal and Behavioural Levels*, Academic Press: New York, pp 265-285.
- Butler, R.B., Diamond, I.T., and Neff, W.D. (1957) Role of auditory cortex in discrimination of changes of frequency. *J. Neurophysiol.* 20, 108-120.
- Elliott, D., Stein, L., and Harrison, M. (1960) Determination of absolute intensity thresholds and frequency difference thresholds in cats. *J. Acoust. Soc. Amer.*, 32, 380-384.
- Heffner, R.S., and Heffner, H.E. (1982) Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Psychol.* 96, 926-944.
- Thompson, R.F. (1960) Function of auditory cortex in cat in frequency discrimination. *J. Neurophysiol.* 23, 321-334.

Table M65-0. Frequency discrimination in several mammal species.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)						
	1	2	3	4	5	6	7
62.5	2.8						
125	7						
200		8.5					
250	8				1.25	0.75	
500	8.5				2.5	1.5	
1000	8.5		23	9	29	6	10.5
2000	15	16.75			84	11	
4000	35				184	36	
8000	100	155			324	80	
16000	238						
32000	575						

Notes:

1- Instrumental shock-avoidance conditioning in a tilt-cage using the descending method of limits. Signals were 40 dB SL, 400 msec repeating tone bursts. Conditioned stimulus was an alternation of frequency between successive bursts. Medians: N=8.

2- Instrumental shock avoidance (barrier crossing in a double grill box) using a method of constant stimuli. Signals were repeating tone bursts, 70 to 80 dB sensation level, one sec in duration. The conditioned stimulus was an alternation of frequency between successive bursts. Means: N=2 for each data point.

In this experiment, extensive lesions of auditory cortex introduced after training had no effect on the frequency discrimination threshold.

3- Instrumental shock avoidance (paw lift) using the method of constant stimuli. Dogs wore earphones. Signals were 60-65 dB sensation level tone bursts of various durations. Data are averages over the thresholds for signal durations from 120 to 900 msec. Data from a single interval "yes-no" paradigm which required the animal to remember the positive stimulus frequency "absolutely" over many seconds. Means: N=3.

Lesions of auditory cortex had little effect on frequency discrimination of long (>100 msec) tones, but raised discrimination thresholds for short duration tones.

4- Same as #3 except that animals were given a repeating tone burst background and were trained to detect a frequency change (an alternation of frequency between successive bursts). Means: N=2.

5- Operant conditioning with a fruit-flavored sugar solution reward using a method of constant stimuli. Signals were free-field, 50 dB sensation level, 100 msec tones with 20 msec rise/fall times for frequencies above 500 Hz, and longer times for the lower frequencies. The conditioned stimulus was an alternation of frequency between successive bursts. Data are for one animal (7 year-old female Indian elephant). This threshold is based on 75% correct detection on the psychometric function for a two-alternative, same-different task.

6- Same as #5 except that the threshold was based on the frequency difference giving a response probability statistically different from chance ($p < 0.01$, one tailed). This tended to correspond to 63% correct on the psychometric function.

7- Instrumental shock avoidance (Brogden-Culler wheel) using the method of constant stimuli. Signal was an alternation of the frequency of a repeating background (40 to 65 dB SPL) between the background frequency and a higher comparison frequency. Three animals were tested but the data were shown for only one animal. The threshold given is an average (50% correct) for pre- and post-operative tests. Using this method, ablation of all known auditory cortex had no effect on the frequency discrimination threshold.

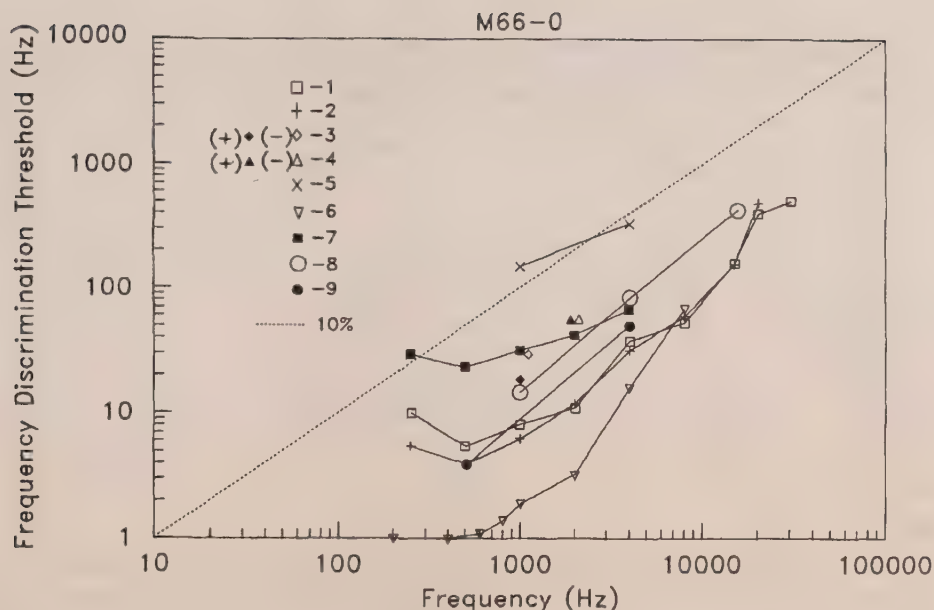


Fig. M66-0. Frequency discrimination in primates.

- 1- *Macaca* sp. - macaque (Stebbins, 1970)
- 2- *Macaca* sp. - macaque (Stebbins, 1973)
- 3- Old World monkeys - see Notes (Sinnott, Petersen, and Hopp, 1985)
- 4- Old World monkeys - see Notes (Sinnott, Owren, and Petersen, 1987)
- 5- *Samiri sciureus* - squirrel monkey (Capps and Ades, 1968)
- 6- *Homo sapiens* - human (Weir, Jesteadt, and Green, 1976)
- 7- *Macaca* sp. - macaque (Moody, May, Cole, and Stebbins, 1986)
- 8- *Macaca mulatta* - rhesus monkey (Heffner and Masterton, 1978)
- 9- *Macaca mulatta* - rhesus monkey (Massopust, Wolin, & Frost, 1971)

Capps, M.J., and Ades, H.W. (1968) Auditory frequency discrimination after transection of the olivocochlear bundle in squirrel monkey. *Exp. Neurol.* 21, 147-158.

Heffner, H. and Masterton, B. (1978) Contribution of auditory cortex to hearing in the monkey (*Macaca mulatta*). In D.J. Chivers and J. Herbert (eds), *Recent Advances in Primatology*, Vol I. Academic Press: New York, pp. 735-754.

Massopust, L., Wolin, L., & Frost, V. (1971) Frequency discrimination thresholds following auditory cortex ablations in the monkey. *J. Aud. Res.* 11, 227-233.

Moody, D., May, B., Cole, D., and Stebbins, W. (1986) The role of frequency modulation in the perception of complex stimuli by primates. *J. Exp. Biol.* 45, 219-232.

Sinnott, J.M., Petersen, M.R., and Hopp, S.L. (1985) Frequency and intensity discrimination in humans and monkeys. *J. Acoust. Soc. Amer.* 78, 1977-1985.

Sinnott, J.M., Owren, M.J., and Petersen, M.R. (1987) Auditory frequency discrimination in primates: Species differences (*Cercopithecus*, *Macaca*, *Homo*). *J. Comp. Psychol.* 101, 126-131.

Stebbins, W.C. (1973) Hearing of Old World monkeys (*Cercopithecinae*). *Amer. J. of Phys. Anthropol.* 38, 357-364.

Stebbins, W.C. (1970) Studies of hearing and hearing loss in the monkey. In W.C. Stebbins (ed), *Animal Psychophysics*. Appleton-Century-Crofts: New York.

Weir, C., Jesteadt, W., and Green, D. (1976) Frequency discrimination as a function of frequency and sensation level. *J. Acoust. Soc. Amer.* 61, 178-184.

Table M66-0. Frequency discrimination in primates.

Frequency (Hz)	Frequency Discrimination					Threshold (Hz)			
	1	2	3	4	5	6	7	8	9
200						1			
250	10	5.5					29		
400						1			
500	5.5	4					23		4
600						1.1			
800						1.4			
1000(+)	8.2	6.3	18.6		150	1.9	31	15	
1000(-)			29.7						
2000(+)	11	12		56		3.2	41		
2000(-)				57					
4000	38	32			333	15.9	66	85	30-70
8000	53	60				68.5			
15000	160	158							
16000								410	
20000	400	490							
30000	510								

Notes:

1- Operant conditioning for food using tracking. Animals contacted a key to initiate a trial and released after the signal onset. Earphones were used. Tone bursts of constant frequency (60 dB SL) were repeated continuously. Signal was the alternation of the frequency of successive bursts. Medians: N=3 (two macaque species).

2- Operant conditioning for food using tracking. Animals contacted a key to initiate a trial, and then a second key shortly after a signal was presented. Earphones were used. Tone bursts of constant frequency and at 40 or 60 dB sensation level were repeated continuously. The signal was the alternation of the frequency of successive tone bursts. Data are means over 40 and 60 dB SL conditions. N=1.

3- *Macaca fuscata* - Japanese macaque, and *Cercopithecus aethiops* - vervet monkey. Same methods as #1. Signal a variable length period of a repeating standard tone (250 msec duration, 10 msec r/f times, 30 dB SL), and a three sec period of frequency alternation for successive bursts. Frequency change was an increase (+) or a decrease (-) from the standard. See Fig. M69-0 for sensation level effects. Means: N=4.

4- *Macaca fuscata* - Japanese macaque, *Macaca mulatta* - rhesus macaque, *Cercopithecus aethiops* - vervet monkey, *Cercopithecus neglectus* - de Brazza monkey. Same methods as #3. Data are for frequency increases (+) and decreases (-) at 2000 Hz (30 dB SL). See Fig. M69-0 for the effect of sensation level. Means: N=6.

5- Animals trained in a WGTA to choose one of two loudspeakers emitting the lower frequency tone bursts for food reward. Method of constant stimuli. Signal bursts at 70 dB SPL (about 70 dB SL), twice per sec with 25 msec r/f times. Cutting the olivocochlear bundle raised discrimination thresholds significantly. Means: N=4.

6- Adaptive two-interval forced-choice for 71% correct. Subjects chose the interval with the higher frequency. 500 msec bursts filtered at signal frequency in a 200 Hz passband. 40 dB SL. See Fig. M69-0 for effects of sensation level. Means: N=4.

7- Methods as in #1 above. Signal a 200 msec repeating tone of constant frequency or a linear FM sweep centered on the indicated frequency. Thresholds defined as the frequency sweep range just discriminable from constant frequency.

8- Conditioned suppression of water tube contact using method of constant stimuli. Signal was change from repeating bursts of constant frequency to bursts alternating in frequency. 500 msec on, 500 msec off, 60 dB SPL, 10-25 msec rise/fall times. N=1.

9- Instrumental shock avoidance using a combination of the method of limits and constant stimuli. Intensity was varied randomly. Means: N=45 or fewer animals.

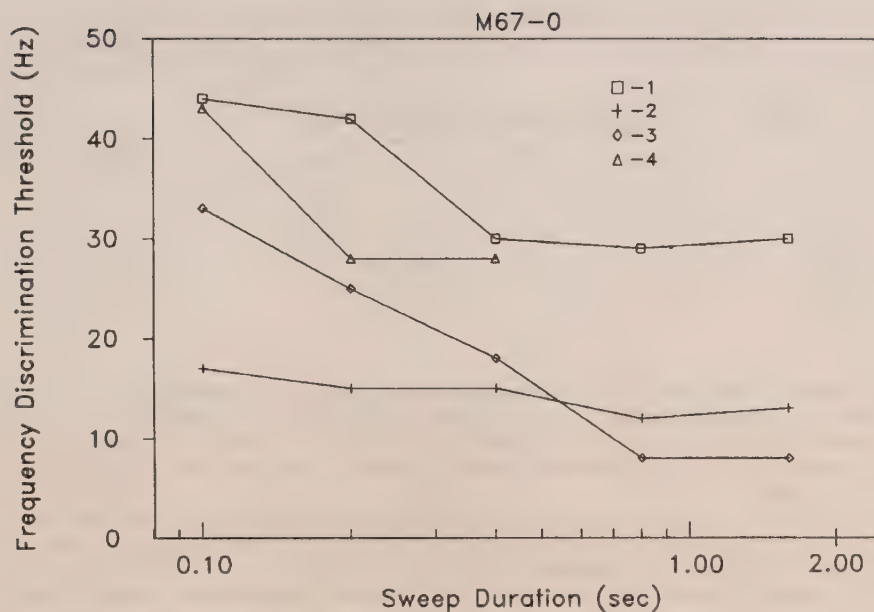


Fig. M67-0. Thresholds for the detection of linear frequency sweeps by *Macaca* sp. (macaque monkey) as a function of sweep duration under three different experimental conditions.

Repeating-Standard Conditions

- 1- Frequency sweep centered on the comparison tone frequency
- 2- Frequency sweep begins to sweep up at the comparison tone frequency

Single-Standard Conditions

- 3- Frequency sweep begins to sweep up at the comparison tone frequency
- 4- Standard frequency varies from trial to trial

Reference:

Moody, D., May, B., Cole, D., and Stebbins, W. (1986) The role of frequency modulation in the perception of complex stimuli by primates. *J. Exp. Biol.* 45, 219-232.

Table M67-0. Thresholds for the detection of linear frequency sweeps by *Macaca* sp. (macaque monkey) as a function of sweep duration under three different experimental conditions.

Sweep Duration (sec)	Frequency Discrimination Threshold (Hz)			
	1	2	3	4
0.1	44	17	33	43
0.2	42	15	25	28
0.4	30	15	18	28
0.8	29	12	8	
1.6	30	13	8	

Notes:

Operant conditioning for a food reward using a tracking psychophysical procedure. Animals were trained to contact a key to initiate a trial and to release after the signal onset. Earphones were used. Threshold was defined as the total sweep range that was just discriminable from a constant frequency standard tone. Medians: N=3 for #1-#3, N=2 for #4.

1- Upon trial initiation, a standard tone of constant frequency was repeated once every 400 msec. This was to be discriminated from an upward linear frequency sweep centered on the standard tone frequency (500 Hz).

2- Upon trial initiation, a standard tone of constant frequency was repeated once every 400 msec. This was to be discriminated from an upward linear frequency sweep which began to sweep up at the standard tone frequency (500 Hz).

3- Upon trial initiation, a standard tone of constant frequency was presented only once. This was to be discriminated from a single presentation of an upward linear frequency sweep which began to sweep up at the standard tone frequency (500 Hz).

4- Upon trial initiation, a standard tone was presented only once. The frequency of this tone varied from trial to trial. This "variable standard" was to be discriminated from an upward linear frequency sweep beginning at 500 Hz.

In general, these data were interpreted to suggest that macaques responded to discrete frequency cues rather than to the presence of modulation *per se*.

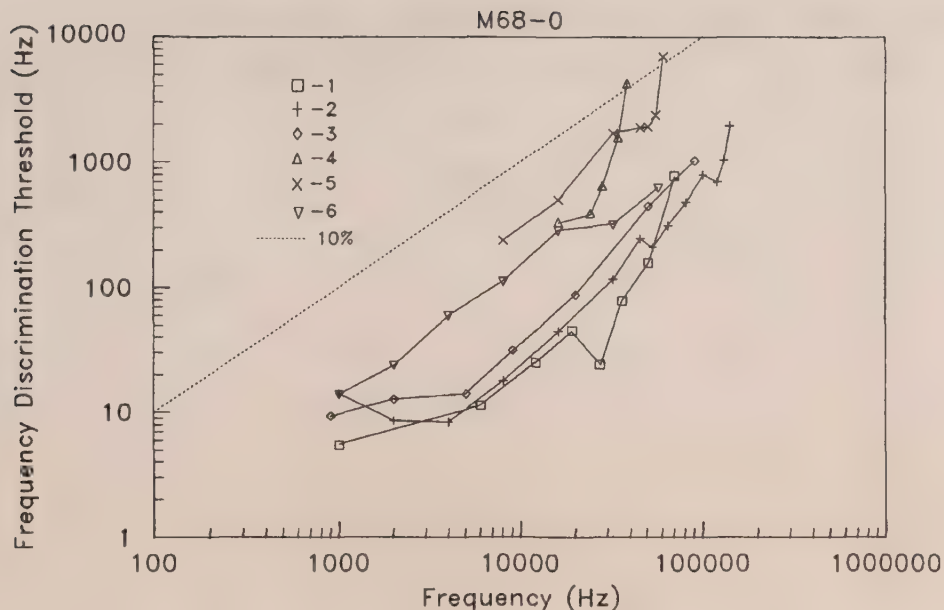


Fig. M68-0. Frequency discrimination thresholds in marine mammals.

- 1- *Tursiops truncatus* - Atlantic bottlenose dolphin (Herman and Arbeit, 1972)
- 2- *Tursiops truncatus* - Atlantic bottlenose dolphin (Thompson and Herman, 1975)
- 3- *Tursiops truncatus* - Atlantic bottlenose dolphin (Jacobs, 1972)
- 4- *Zalophus californianus* - California sea lion (Schusterman and Moore, 1978b)
- 5- *Phoca hispida* - ringed seal (Terhune and Ronald, 1976)
- 6- *Phoca vitulina* - common seal (Mohl, 1967)

References:

- Herman, L.M., and Arbeit, W.R. (1972) Frequency difference limens in the bottlenose dolphin: 1-70 kc/s. *J. Aud. Res.* 2, 109-120.
- Jacobs, D.W. (1972) Auditory frequency discrimination in Atlantic bottlenose dolphin, *Tursiops truncatus* Montague: A preliminary report. *J. Acoust. Soc. Amer.* 52, 696-698.
- Mohl, B. (1967) Frequency discrimination in the common seal. In V.A. Albers (ed), *Underwater Acoustics*. Plenum: New York, pp. 43-54.
- Schusterman, R.J., and Moore, P.W.B. (1978b) The upper limit of underwater auditory frequency discrimination in the California sea lion. *J. Acoust. Soc. Amer.* 63, 1591-1595.
- Terhune, J.M. and Ronald, K. (1976) The upper frequency limit of ringed seal hearing. *Can. J. Zool.* 54, 1226-1229.
- Thompson, R.K., and Herman, L.M. (1975) Underwater frequency discrimination in the bottlenose dolphin (1-140 kHz) and the human (1-8 kHz). *J. Acoust. Soc. Amer.* 57, 943-948.

Table M68-0. Frequency discrimination thresholds in marine mammals.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)					
	1	2	3	4	5	6
900			9.4			
1000	5.5	14.2				14
2000		8.6	12.8			24
4000		8.4				60
5000			14.1			
6000	11.4					
8000		18			240	112
9000			31.7			
12000	25.2					
16000		45		336	504	288
19000	45.6					
20000			88.5			
24000				396		
27000	24.3					
28000				652		
32000		118			1712	320
34000				1581		
36000	79.2					
38000				4256		
45000		248			1890	
50000	160		450		1925	
53000		212				
55000					2393	
57000						627
60000					6990	
64000		314				
70000	784					
80000		480				
90000			1038			
100000		800				
120000		708				
130000		1053				
140000		1960				

Notes:

1- Operant conditioning for a food reward using tracking. An observing response initiated two successive 2.5 sec signals from different loudspeakers (a pure tone and the other a 2 Hz sinusoidally frequency modulated tone). Levels were 26 to 47 dB re: 1 dyne cm⁻². Nosing a paddle associated with the pure tone was rewarded. N=1.

2- Same methods as in #1. Signal levels 40 to 100 dB sensation level. N=1.

3- Same as #1. Sounds from one speaker, 15 to 33 dB re: 1 dyne cm⁻². N=1.

4- Operant conditioning (vocalization) for a food reward using a tracking procedure. A trial consisted of two, 1 sec signals at 20 to 30 dB sensation level. The first was always the "standard" tone and the second was either the same or lower frequency than the standard. Barking indicated a frequency difference. N=1.

5- Same method as in Fig. M34-0, #3. Animal discriminated between pure tone pulses and tones frequency modulated at 2.5 Hz, 30 to 60 dB sensation level. Means: N=2.

6- Same method as in Fig. M34-0, #2. The signal was a set of 500 msec constant frequency bursts or bursts alternating in frequency (30 to 70 dB sensation level). The intensity of each burst was randomly varied. Means: N=2.

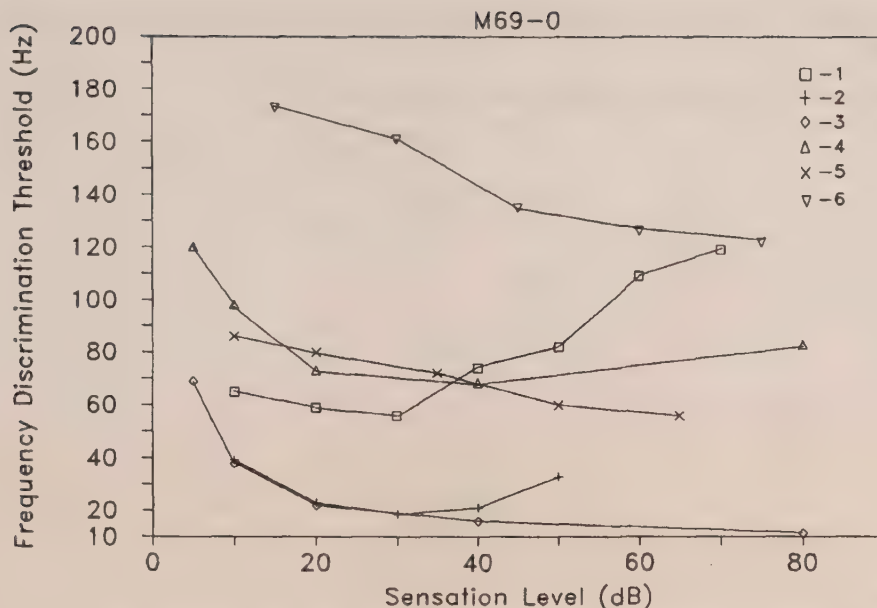


Fig. M69-0. The effect of sensation level on frequency discrimination in several species.

- 1- *Macaca fuscata* - Japanese macaque
Macaca mulatta - rhesus monkey
Cercopithecus aethiops - vervet monkey
Cercopithecus neglectus - de Brazza monkey (2000 Hz) (Sinnott, Owren, and Petersen, 1987)
- 2- *Macaca fuscata* - Japanese macaque
Cercopithecus aethiops - vervet monkey (1000 Hz) (Sinnott, Petersen, and Hopp, 1985)
- 3- *Homo sapiens* - human (4000 Hz) (Weir, Jesteadt, and Green, 1976)
- 4- *Homo sapiens* - human (8000 Hz) (Weir, Jesteadt, and Green, 1976)
- 5- *Mus musculus* - laboratory mouse (5000 Hz) (Ehret, 1975b)
- 6- *Mus musculus* - laboratory mouse (15000 Hz) (Ehret, 1975b)

References:

- Ehret, G. (1975b) Frequency and intensity difference limens and nonlinearities in the ear of the housemouse (*Mus musculus*). *J. Comp. Physiol.* 102, 321-336.
- Sinnott, J.M., Petersen, M.R., and Hopp, S.L. (1985) Frequency and intensity discrimination in humans and monkeys. *J. Acoust. Soc. Amer.* 78, 1977-1985.
- Sinnott, J.M., Owren, M.J., and Petersen, M.R. (1987) Auditory frequency discrimination in primates: Species differences (*Cercopithecus*, *Macaca*, *Homo*). *J. Comp. Psychol.* 101, 126-131.
- Wier, C., Jesteadt, W., and Green, D. (1976) Frequency discrimination as a function of frequency and sensation level. *J. Acoust. Soc. Amer.* 61, 178-184.

Table M69-0. The effect of sensation level on frequency discrimination in several species.

Duration (msec)	Frequency Discrimination Threshold (Hz)					
	1	2	3	4	5	6
5			68.9	120.1		
10	65	38	37.7	98.2	86	
15						173
20	59	23	21.8	73.1	80	
30	56	18.6				161
35					72	
40	74	21	15.9	68.5		
45						135
50	82	32.8			60	
60	109					126
65					56	
70	119					
75						122
80			11.4	82.8		

Notes:

1- Operant conditioning for a food reward using a tracking psychophysical procedure. Animals were trained to contact a key to initiate a trial and to release after the signal onset. Earphones were used. Tone bursts of constant frequency (2000 Hz) were repeated continuously as a background stimulus. The conditioned stimulus was the alternation of the frequency of successive tone bursts. Means: N=6.

2- Same methods as in #1. Frequency of 1000 Hz. Note for the monkeys that lowest thresholds are found at 30 dB sensation level. Means: N=2.

3-4- Adaptive two-interval forced-choice for 71% correct. Subjects decided which interval contained the higher frequency. Signals were 500 msec square-gated bursts filtered at the signal frequency in a 200 Hz passband. Similar data were collected at several other frequencies. Note that the frequency discrimination threshold is generally a decreasing function of sensation level for the human. Means: N=4.

3- 400 Hz signal frequency

4- 1000 Hz signal frequency

5-6- Operant conditioning for a water reward using the method of constant stimuli. Animals learned to approach and lick a drinking tube during frequency increments. Signals were 100 msec tone bursts (10 msec rise/fall times) repeated 5 times per sec. The conditioned stimulus was an alternation of the frequency of successive bursts. Similar data were collected at several other frequencies (not shown here). Note that for the mouse, the frequency discrimination threshold is a decreasing function of sensation level. Means: N=7.

5- 5000 Hz signal frequency

6- 15000 Hz signal frequency

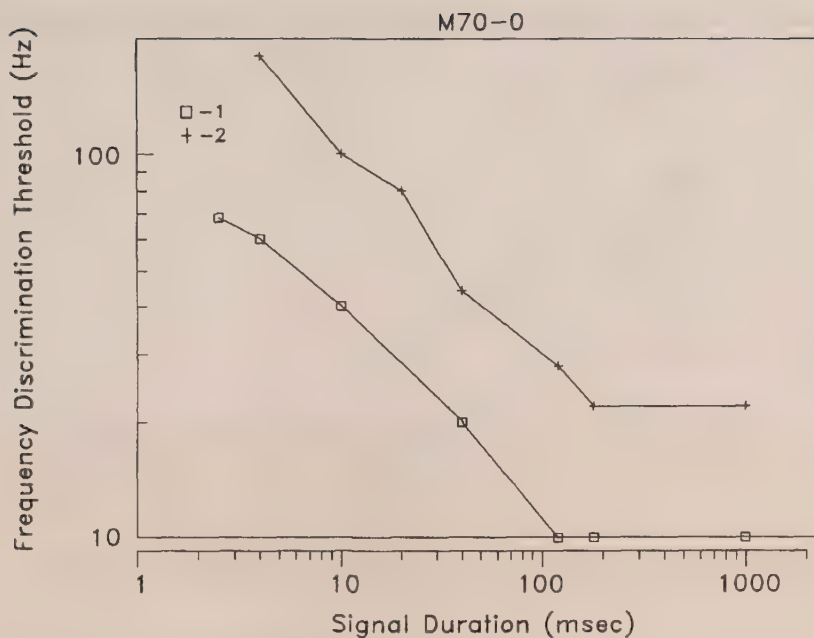


Fig. M70-0. Frequency discrimination in *Canis canis* (dog) as a function of duration.

- 1- Relative frequency change condition
- 2- Absolute frequency memory condition.

Reference:

Baru, A.V. (1971) Behavioral thresholds and frequency difference limen as a function of sound duration in dogs deprived of the auditory cortex. In G.V. Gersuni (ed), *Sensory Processes at the Neuronal and Behavioural Levels*, Academic Press: New York, pp. 265-285.

Table M70-0. Frequency discrimination in *Canis canis* (dog) as a function of duration.

Duration (msec)	Frequency Discrimination Threshold (Hz)	
	1	2
2.5	68	
4	60	180
10	40	100
20		80
40	20	44
120	10	28
180	10	22
1000	10	22

Notes:

1- Instrumental shock avoidance (paw lift) using the method of constant stimuli. Dogs wore earphones. Signals were 60-65 dB sensation level tone bursts of various durations. Animals were given a repeating tone burst background and were trained to detect a frequency change (an alternation of frequency between successive bursts). Means: N=2.

2- Same as above except that data were obtained in a single interval "yes-no" paradigm which required the animal to remember the positive stimulus frequency "absolutely" over many seconds. Means: N=3.

In these experiments, auditory cortex lesions increased frequency discrimination thresholds for signal durations less than 100 msec, but not for longer durations.

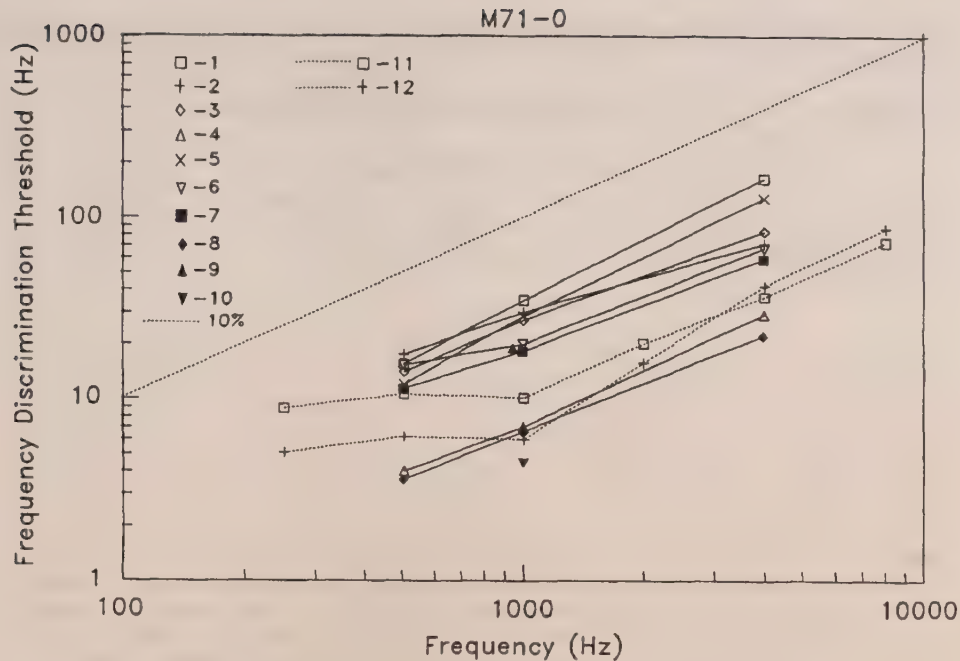


Fig. M71-0. Frequency discrimination thresholds in *Homo sapiens* (human) infants and adults.

- 1- 3 month-old infants, 40 dB sensation level
- 2- 6 month-old infants, 40 dB sensation level
- 3- 12 month-old infants, 40 dB sensation level
- 4- adults, 40 dB sensation level
- 5- 3 month-old infants, 80 dB sensation level
- 6- 6 month-old infants, 80 dB sensation level
- 7- 12 month-old infants, 80 dB sensation level
- 8- adults, 80 dB sensation level
- Olsho and Halpin, 1987a
- 9- 7-9 month-old infants, 60 dB SPL
- 10- adults, 60 dB SPL
- Sinnott and Aslin, 1985
- 11- 5-8 month-old infants, 70 dB sensation level
- 12- Adults tested similarly

References:

- Olsho, L.W. (1984) Infant frequency discrimination. *Infant Behav. and Develop.* 7, 27-35.
- Olsho, L.W., and Halpin, C.F. (1987a) Level and age effects in infant frequency discrimination. *J. Acoust. Soc. Amer.* 82, 454-464.
- Sinnott, J.M., and Aslin, R.N. (1985) Frequency and intensity discrimination in human infants and adults. *J. Acoust. Soc. Amer.* 78, 1986-1992.

Table M71-0. Frequency discrimination thresholds in *Homo sapiens* (human) infants and adults.

Frequency (Hz)	Frequency Discrimination Threshold (Hz)									
	1	2	3	4	5	6	7	8	9	10
500	15.5	17.5	14	4	12	15.3	12	3.7		
1000	35	30	27	7	28.5	20	19.5	6.8	20.3	4.6
4000	164	72	84	29.2	128	68	66	24		
	11	12								
250	8.75	5								
500	10.5	6.1								
1000	10	5.9								
2000	20	15.6								
4000	36.4	42								
8000	72.8	86.4								

Notes:

1-8- Operant response for a visual reward using the method of constant stimuli. Infant was rewarded for some response (usually a head-turn) in the presence of a signal with the chance to watch an illuminated motorized toy. An observer decided on any given trial whether the infant responded using whatever criteria the observer could use. The reward to the infant followed the correct detection by the observer. Adults were tested similarly. Signals were 500 msec tone bursts repeated once per sec with 10 msec rise/fall times delivered to the right ear over headphones. The conditioned stimulus was an alternation of the frequency between successive bursts. Means: N=12 (adults), N=35 3-month olds, N=34 6-month olds, N=30 12-month olds.

At 4000 Hz, the thresholds for 6- and 12-month old infants did not differ significantly from adults.

9-10- Go, no-go operant head-turn for a visual reward using a tracking procedure. An observer decided whether or not the infant responded with a head-turn. Signals were 60 dB SPL, 1000 Hz tones, 330 msec in duration with 10 msec rise/fall times repeated every 750 msec. The conditioned stimulus was an alternation of the frequency (increments) between successive bursts. Thresholds were also obtained for frequency decrements. These did not differ significantly from the thresholds for increments. Means: N=6 adults, N=5 7-9 month-olds.

11-12- Operant conditioning of a head-turn toward a mechanical toy using "two-down, one-up" rule in a tracking procedure. An independent, "blind" observer decided when head-turns occurred. Background signal was repeating 500 msec tone bursts (20 msec rise/fall times), once per sec. Conditioned stimulus was the change of the frequency of the repeating tone. Stimuli presented at 70 dB sensation level. Means: N=18 infants ranging in age from 5 months, 3 days to 7 months, 18 days; N=6 adults.

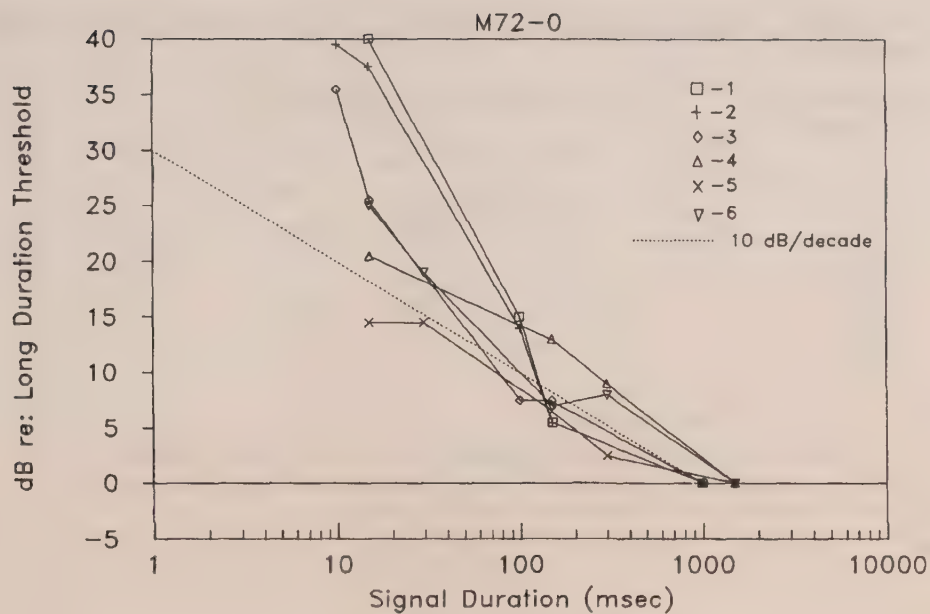


Fig. M72-0. Temporal summation at threshold for *Macaca mulatta* (rhesus monkey) (Clack, 1966).

- 1- 250 Hz signal
- 2- 500 Hz
- 3- 1000 Hz
- 4- 2000 Hz
- 5- 4000 Hz
- 6- 8000 Hz

Reference:

Clack, T.D. (1966) Effect of signal duration on auditory sensitivity of humans and monkeys (*Macaca mulatta*). J. Acoust. Soc. Amer. 40, 1140-1146.

Table M72-0. Temporal summation at threshold for *Macaca mulatta* (rhesus monkey)
(Clack, 1966).

Signal Duration (msec)	dB re: Threshold at Long Duration					
	1	2	3	4	5	6
10		39.5	35.5			
15	40	37.5	25.5	20.5	14.5	25
30					14.5	19
100	15	14	7.5			
150	5.5	5.5	7.5	13	6.5	7
300				9	2.5	8
1000	0	0	0			
1500				0	0	0

Notes:

Instrumental shock avoidance ("single lever technique") using a tracking procedure. Signals had 10 msec rise/fall time. Earphones (monaural) were used. Humans also tested (data not shown here). Means: N=2.

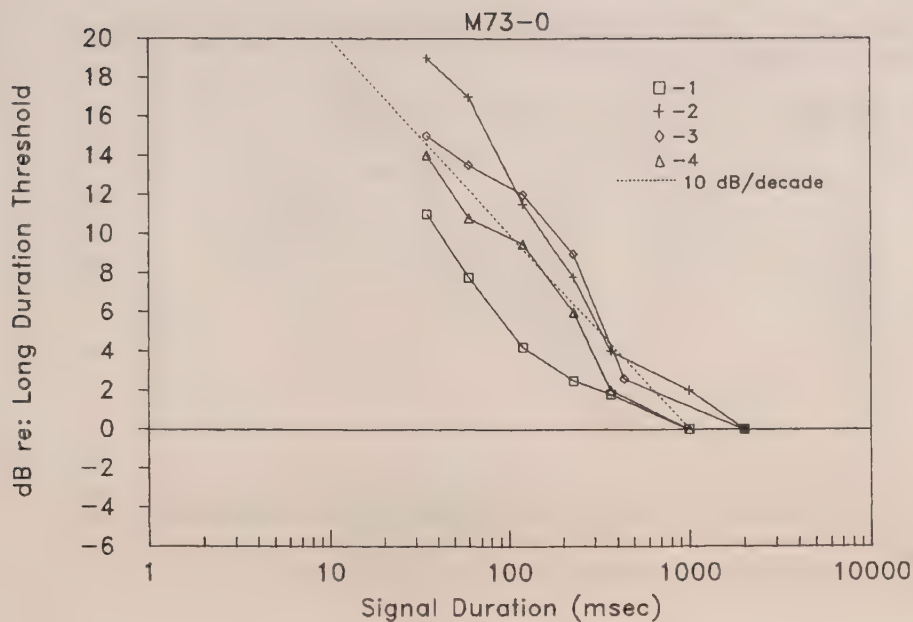


Fig. M73-0. Temporal summation at threshold for *Cercopithecus mitis* (blue monkey) (Brown and Maloney, 1986).

- 1- 250 Hz signal frequency
- 2- 800 Hz
- 3- 1600 Hz
- 4- 4000 Hz

Reference:

Brown, C.H. and Maloney, C.G. (1986) Temporal integration in two species of Old World monkeys: Blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Cercocebus albigena*). J. Acoust. Soc. Amer. 79, 1058-1064.

Table M73-0. Temporal summation at threshold for *Cercopithecus mitis* (blue monkey) (Brown and Maloney, 1986).

Signal Duration (msec)	dB re: Threshold at Long Duration			
	1	2	3	4
35	11	19	15	14
60	7.8	17	13.5	10.8
120	4.2	11.5	12	9.5
230	2.5	7.8	9	6
370	1.8	4		2
440			2.6	
1000	0	2		0
2000	0	0	0	0

Notes:

Operant conditioning for a food reward using a tracking procedure. Animals were trained to press a lever to initiate a trial (observing response) and to hold the lever until a signal was detected. Signals had 20 msec rise/fall times. Human observers also similarly tested. Time constant calculated to be maximum at 800 Hz (340 msec). Means: N=2.

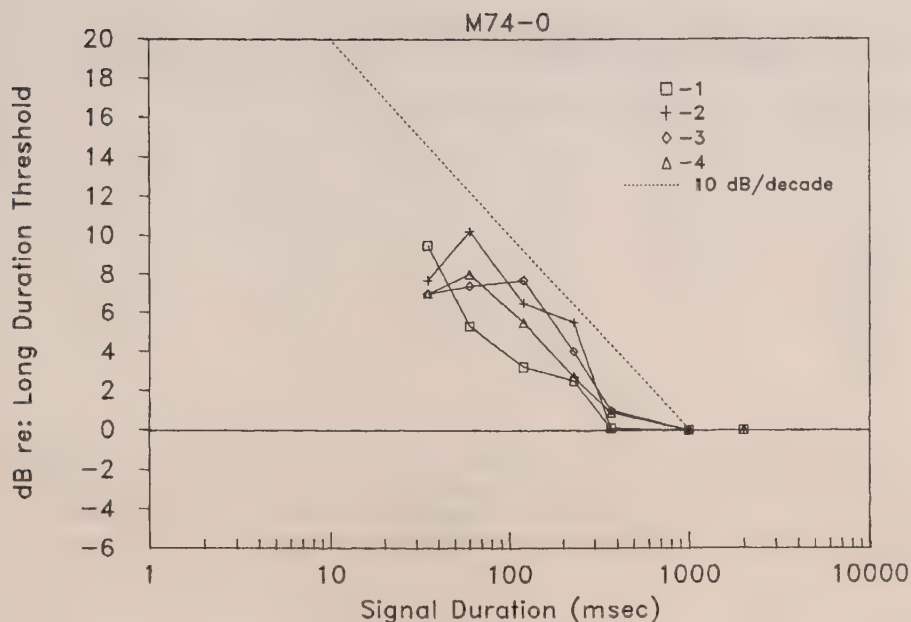


Fig. M74-0. Temporal summation at threshold for *Cercopithecus albigena* (grey-cheeked mangabey) (Brown and Maloney, 1986).

- 1- 250 Hz signal frequency
- 2- 800 Hz
- 3- 1600 Hz
- 4- 4000 Hz

Reference:

Brown, C.H. and Maloney, C.G. (1986) Temporal integration in two species of Old World monkeys: Blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Cercopithecus albigena*). J. Acoust. Soc. Amer. 79, 1058-1064.

Table M74-0. Temporal summation at threshold for *Cercocebus albigena* (grey-cheeked mangabey) (Brown and Maloney, 1986).

Signal Duration (msec)	dB re: Threshold at Long Duration			
	1	2	3	4
35	9.5	7.7	7	7
60	5.3	10.2	7.4	8
120	3.2	6.5	7.7	5.5
230	2.5	5.5	4	2.7
370	0.1	0.1	1	0.9
1000	0	0	0	0
2000	0	0		0

Notes:

Operant conditioning for a food reward using a tracking procedure. Animals were trained to press a lever to initiate a trial (observing response) and to hold the lever until a signal was detected. Signals had 20 msec rise/fall times. Human observers also similarly tested. Time constant calculated to be maximum at 800 Hz (340 msec). Means: N=2.

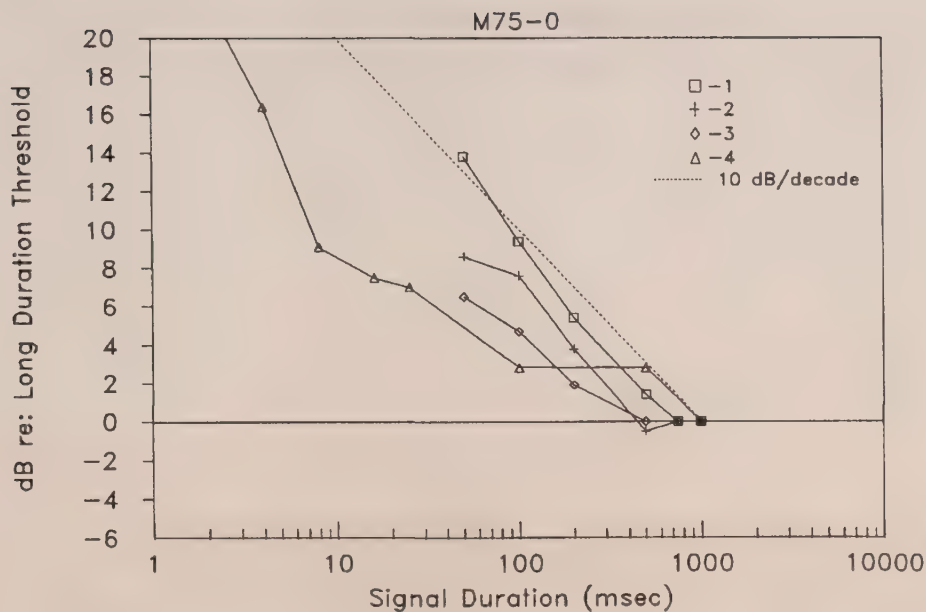


Fig. M75-0. Temporal summation at threshold for *Felis catus* (cat).

1- 250 Hz signal frequency

2- 1000 Hz

3- 8000 Hz

Costalupes, 1983

4- 1000 Hz signal frequency

Cranford and Igarashi, 1977

References:

Cranford, J.L., and Igarashi, M. (1977) Effects of auditory cortex lesions on temporal summation in cats. *Brain. Res.* 136, 559-564.

Costalupes, J.A. (1983) Temporal integration of pure tones in the cat. *Hear. Res.* 9, 43-54.

Table M75-0. Temporal summation at threshold for *Felis catus* (cat).

Signal Duration (msec)	dB re: Threshold at Long Duration			
	1	2	3	4
2				22
4				16.4
8				9.1
16				7.5
25				7
50	13.8	8.6	6.5	
100	9.4	7.6	4.7	2.8
200	5.4	3.8	1.9	
500	1.4	-0.5	0	2.8
750	0	0	0	
1000	0	0	0	0

Notes:

1-3- Operant conditioning for a food reward using a tracking procedure. Animals were trained to nose a panel (observing response) to initiate a trial, and to hold the panel until a signal was detected. Signals had 10 msec rise/fall times. Time constants decreased monotonically from about 480 msec at 125 Hz to about 130 msec at 8000 Hz. Data also collected at 125, 500, 2000 and 4000 Hz (not shown here). Means: N=3.

4- Instrumental shock avoidance (shuttle box) using a modified method of limits. Signals were 1000 Hz tone pulses with 1 msec rise/fall times repeated about once per sec. Lesions of the auditory cortex had no effect on temporal summation. N=1.

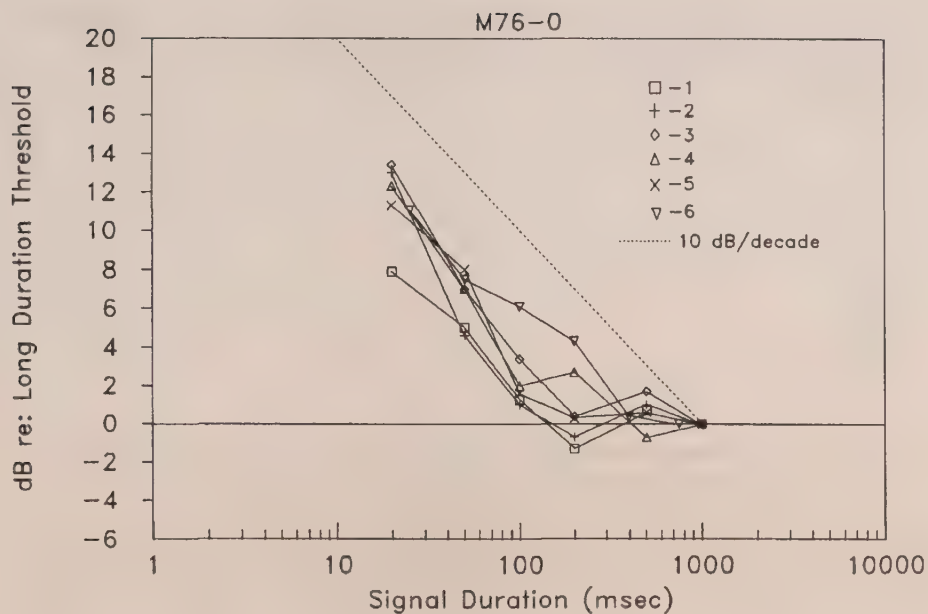


Fig. M76-0. Temporal summation at threshold in *Chinchilla laniger* (chinchilla).

- 1- 500 Hz signal frequency
- 2- 750 Hz
- 3- 1000 Hz
- 4- 2000 Hz
- 5- 4000 Hz

Wall, Ferraro, and Dunn, 1981

- 6- 1000 Hz signal frequency
- Henderson, 1967

References:

- Henderson, D. (1969) Temporal summation of acoustic signals by the chinchilla. *J. Acoust. Soc. Amer.* 46, 474-475.
- Wall, L.G., Ferraro, J.A., and Dunn, D.E. (1981) Temporal integration in the chinchilla. *J. Aud. Res.* 21, 29-37.

Table M76-0. Temporal summation at threshold in *Chinchilla laniger* (chinchilla).

Signal Duration (msec)	dB re: Threshold at Long Duration					
	1	2	3	4	5	6
20	7.9	13	13.4	12.3	11.3	
25						11.05
50	5	4.6	7	7	8	7.5
100	1.3	1	3.4	2	1.6	6.1
200	-1.3	-0.7	0.4	2.7	0.3	4.3
400						0.4
500	0.7	1	1.7	-0.7	0.6	
750						0
1000	0	0	0	0	0	

Notes:

1-5- Instrumental shock avoidance (shuttle box) using the method of limits. Signals had 5 msec rise/fall times and their duration defined as in Dallos and Olsen (1964). Signal bursts separated by 500 msec of silence. Means: N=5.

6- Instrumental shock avoidance (shuttle box) using the method of limits. Signals (2000 Hz) had 5 msec rise/fall times. Signal bursts separated by 500 msec of silence. Noise exposure reduced the difference between thresholds at 25 msec and 750 msec to about zero when the animals were tested a few minutes after the exposure. At 19 days following the exposure, the threshold difference was about 6 dB. Means: N=2.

See also M80-0 for another set of temporal summation data for the chinchilla.

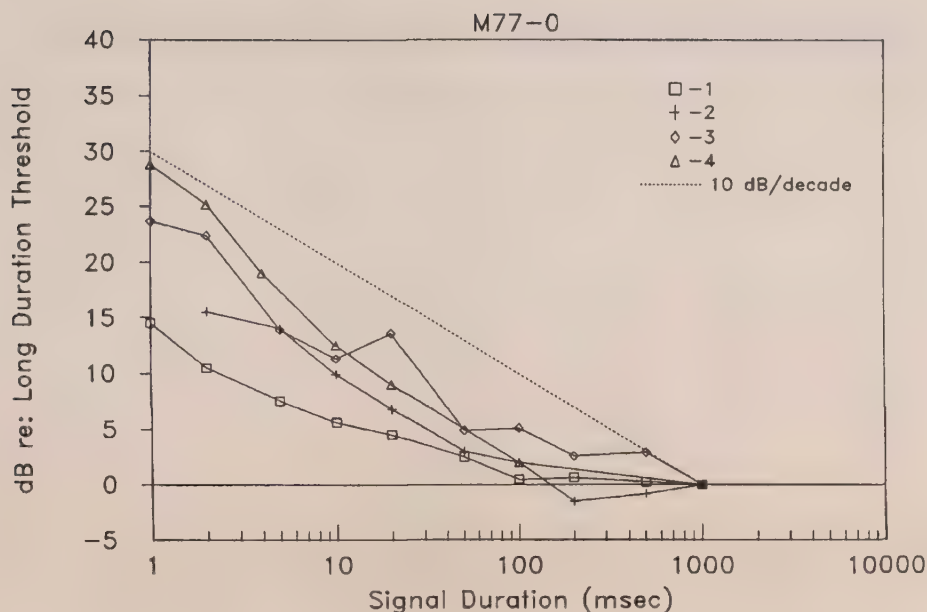


Fig. M77-0 Temporal summation at threshold for *Tursiops truncatus* (bottlenose porpoise) and *Canis canis* (dog).

1- 45 kHz signal frequency

2- 20 kHz signal frequency

3- 4 kHz signal frequency

Tursiops truncatus - bottlenose porpoise (Johnson, 1968a)

4- 1 kHz signal frequency

Canis canis - dog (Baru, 1971)

References:

- Baru, A.V. (1971) Behavioral thresholds and frequency difference limen as a function of sound duration in dogs deprived of the auditory cortex. In G.V. Gersuni (ed), *Sensory Processes at the Neuronal and Behavioural Levels*, Academic Press: New York, pp. 265-285.
- Johnson, C.S. (1968a) Relation between absolute threshold and duration-of-tone pulses in the bottlenosed porpoise. *J. Acoust. Soc. Amer.* 43, 757-763.

Table M77-0. Temporal summation at threshold for *Tursiops truncatus* (bottlenose porpoise) and *Canis canis* (dog).

Signal Duration (msec)	dB re: Threshold at Long Duration			
	1	2	3	4
1	14.5		23.7	28.8
2	10.5	15.5	22.4	25.2
4				19
5	7.5	14	13.9	
10	5.6	9.9	11.3	12.5
20	4.5	6.8	13.6	9
50	2.5	3	4.9	
100	0.46	2	5.1	2
200	0.66	-1.5	2.6	
500	0.26	-0.8	2.9	
1000	0	0	0	0

Notes:

1-3- Operant conditioning for a food reward using a tracking procedure. Animals were trained to push a lever to initiate a trial (observing response) and to move to and press another lever when the signal was detected. Signals had rise/fall times equivalent to two or three cycles of the stimulus tone. Data were also obtained at signal frequencies of 0.25, 1, and 100 kHz (not shown here). Time constants ranged from 220 msec at 4 kHz to 30 msec at 45 kHz. N=1.

4- Instrumental shock avoidance (paw lift) using the method of descending limits. Dogs wore earphones. Signals were 1000 Hz tone bursts gated on at zero degrees phase. Lesions of the auditory cortex caused an elevation of thresholds for signal durations less than about 20 msec. Means: N=14.

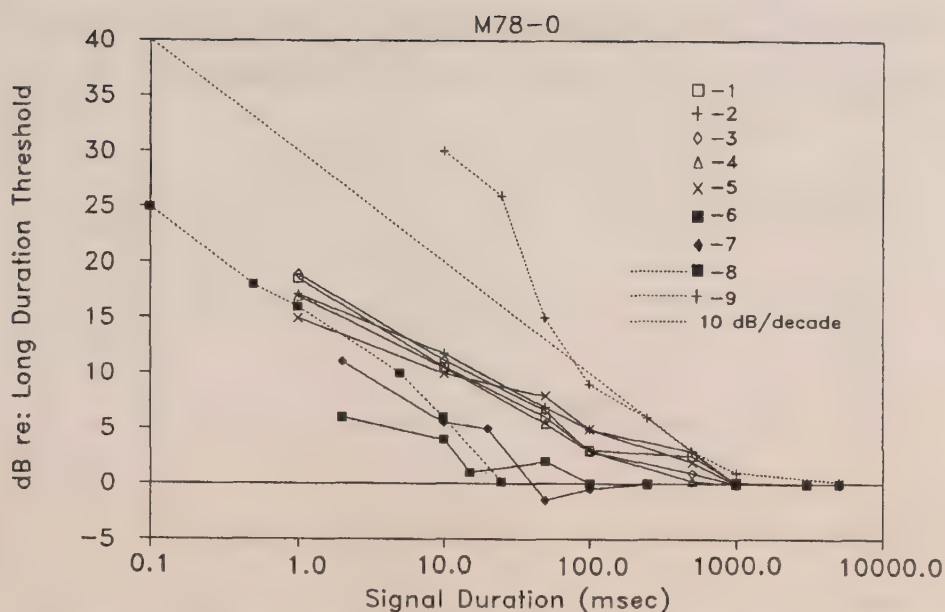


Fig. M78-0. Temporal summation at threshold for a mouse and three bat species.

1- 5 kHz signal frequency

2- 15 kHz

3- 40 kHz

4- 80 kHz

5- Noise

Mus musculus - house mouse (Ehret, 1976a)

6- 12 kHz signal in quiet

7- 12 kHz signal in noise

Rousettus aegyptiacus - a fruit bat (Suthers and Summers, 1980)

8- 40 kHz signal in quiet

Myotis oxygnathus - a large, little brown bat (Ayrappet'yants, and Konstantinov, 1974)

9- 83.5 kHz signal in quiet

Rhinolophus ferrumequinum - horseshoe bat (Ayrappet'yants, and Konstantinov, 1974)

References:

- Ayrappet'yants, E. Sh., and Konstantinov, A.I. (1974) Echolocation in Nature. An English translation of the National Technical Information Service, Springfield, VA, JPRS 63328-1 and -2.
- Ehret, G. (1976a) Temporal auditory summation for pure tones and white noise in the house mouse (*Mus musculus*). J. Acoust. Soc. Amer. 59, 1421-1427.
- Suthers, R.A., and Summers, C.A. (1980) Behavioral audiogram and masked thresholds of the megachiropteran echolocating bat, *Rousettus*. J. Comp. Physiol. 136, 227-233.

Table M78-0. Temporal summation at threshold for a mouse and three bat species.

Signal Duration (msec)	dB re: Threshold at Long Duration								
	1	2	3	4	5	6	7	8	9
0.1								25	
0.5								18	
1	18.6	17.2	19	17	15			16	
2						6	11		
5								10	
10	10.6	11.8	11.2	10.5	10	4	5.5	6	30
15						1			
20							5		
25								0.2	26
50	6.1	7	6.7	5.5	8	2	-1.5		15
100	3.1	5	3	3	5	0	-0.5		9
250							0	0	6
500	2.6	3	1	0.3	2				3
1000	0.2	0	0	0	0			0	1
3000	0	0	0	0	0				
5000								0	0.3

Notes:

1-5- Two methods were used: classical conditioning of eyelid closing (used only for noise thresholds), and operant conditioning for a water reward (approach and licking of drinking tube). The author stated that the two methods gave the same results. A modified method of limits was used. Rise/fall times ranged from 100 msec for 1000 msec tones, to 5 msec for 10 msec tones. (The statement in the paper that the rise/fall time was 2 msec for 1 msec duration tones is likely an error.) Data were obtained at 12 frequencies from 1 to 120 kHz. The duration at which threshold became independent of further increases in duration varied from 115 msec at 120 kHz to 1255 msec at 10 kHz (and was 1230 msec for noise). Means: N=8 (tones) and N=7 (noise).

6-7- Operant conditioning for a food reward using the descending method of limits. Animals were trained to hang from the ceiling of its cage as an observing response, and to wait a variable period for a tone presentation. If the animal left its platform and went to a feeding area within five sec of the tone presentation, it was rewarded with a piece of fruit. Signals were 100 msec tone bursts with 20 msec rise/fall times repeated twice per sec. N=1.

6- In the quiet.

7- Continuous masking noise at 31.7 dB spectrum level.

8-9- These data are reported in the review paper referenced as if for the first time. Operant conditioning for a food reward using a method of descending limits. Animals were trained to move toward (left or right) the source of the signal.

These data were taken from Fig. 41 in the reference. This figure was drawn with a wildly improbable, non-linear abscissa, and the functions shown here are based on the most probable interpretation of the axis.

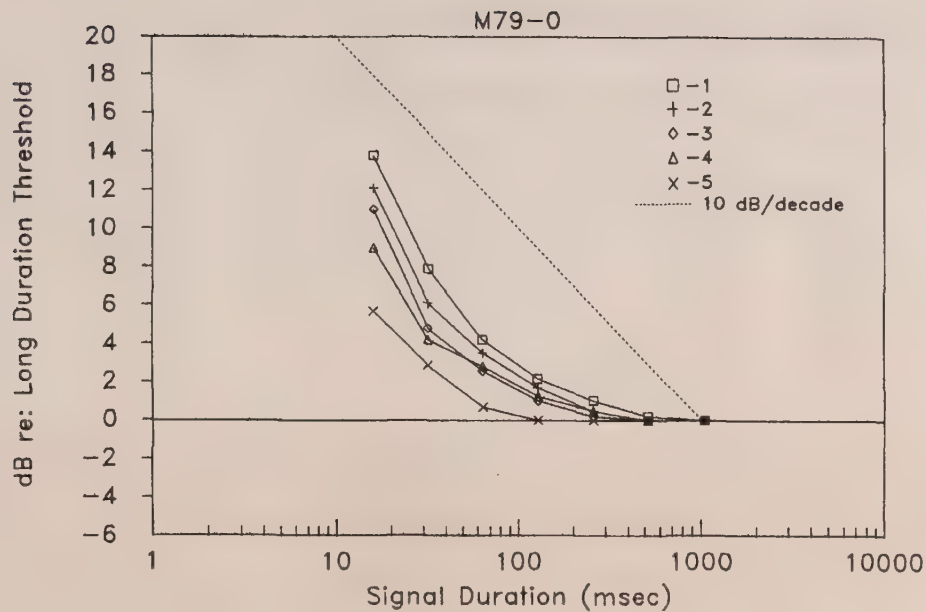


Fig. M79-0. Temporal summation at threshold for *Homo sapiens* (human) (Watson and Gengel, 1969).

- 1- 250 Hz signal
- 2- 500 Hz
- 3- 1000 Hz
- 4- 2000 Hz
- 5- 4000 Hz

Reference:

Watson, C.S., and Gengel, R.W. (1969) Signal duration and signal frequency in relation to auditory sensitivity. *J. Acoust. Soc. Amer.* 46, 989-997.

Table M79-0. Temporal summation at threshold for *Homo sapiens* (human) (Watson and Gengel, 1969).

Signal Duration (msec)	dB re: Long Duration Threshold				
	1	2	3	4	5
16	13.8	12.1	11	9	5.7
32	7.9	6.1	4.8	4.2	2.85
64	4.2	3.5	2.55	2.8	0.68
128	2.15	1.7	1	1.25	0
256	1.05	0.5	0.2	0.5	0
512	0.2	0	0	0	0
1048	0	0	0	0	0

Notes:

Method of adjustment. Subjects were instructed to adjust the level of the signal (tone bursts with 5 msec rise/fall times separated by 400 msec of silence) to be just detectable. Signals were further bandpass filtered with the filter centered on the signal frequency with a bandwidth of plus and minus 20% of the signal frequency. Right ear. Means: N=7.

Time constants (as defined by Plomp and Bouman, 1959) ranged from 180 msec at 125 Hz to 60 msec at 4000 Hz. The authors point out that at short signal durations at low frequencies tend to spread spectral energy that may be detected by channels tuned off of (above) the signal frequency. A demonstration experiment at 125 Hz showed that with short rise times and no filtering, there appeared to be no temporal summation (a flat function of signal duration). This was due to a reduction of the thresholds at the short signal durations. Adding a wide band noise to the experiment (masking the detection of low level energy spread to other frequencies) restored the duration-intensity trade characteristic of temporal summation.

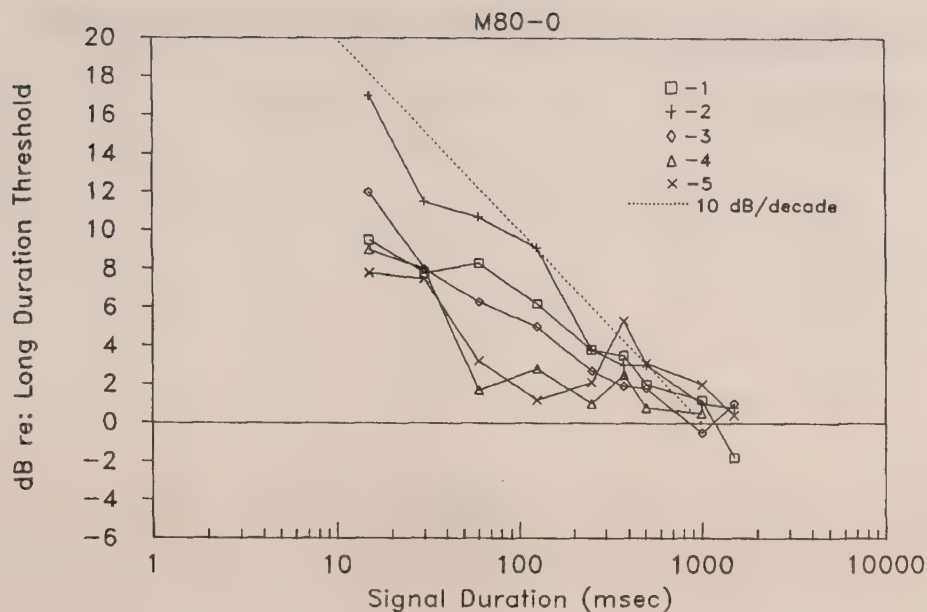


Fig. M80-0. Temporal summation at threshold for *Chinchilla laniger* (chinchilla) (Clark and Bohne, 1986).

- 1- 250 Hz signal
- 2- 715 Hz
- 3- 2000 Hz
- 4- 4000 Hz
- 5- 8000 Hz

Reference:

Clark, W.W., and Bohne, B.A. (1986) Cochlear damage: Audiometric correlates. In M.J. Collins, T.J. Glatke, and L.A. Harker (eds), *Sensorineural Hearing Loss: Mechanisms, Diagnosis, and Treatment*. University of Iowa Press: Iowa City.

Table M80-0. Temporal summation at threshold for *Chinchilla laniger* (chinchilla)
(Clark and Bohne, 1986).

Signal Duration (msec)	dB re: Long Duration Threshold				
	1	2	3	4	5
15	9.5	17	12	9	7.8
30	7.8	11.5	8	8	7.5
60	8.3	10.7	6.3	1.7	3.2
125	6.2	9.1	5	2.8	1.2
250	3.8	3.8	2.7	1	2.1
375	3.5	3	1.9	2.5	5.3
500	2	3	1.8	0.8	3.1
1000	1.2	1	-0.5	0	2
1500	-1.8	0.8	1		0.4

Notes:

Operant conditioning for a food reward using a tracking psychophysical procedure. Animals were trained to depress an observing lever and hold it for a variable period (1-6 sec). If the animal released the lever during the 2-sec tone trial, it was reinforced with food. Left ear destroyed. Duration defined as the time between half-power points on signal rise and fall (10 msec). Means: N=4.

Time constants (calculated according to the method of Plomp and Bouman, 1959) were as follows:

250 Hz	303 msec
715 Hz	420 msec
2000 Hz	209 msec
4000 Hz	105 msec
8000 Hz	153 msec

After a permanent threshold shift of at least 30 dB (caused by noise exposure), thresholds for 715 Hz signal showed significantly less temporal summation over signal duration (lower slope).

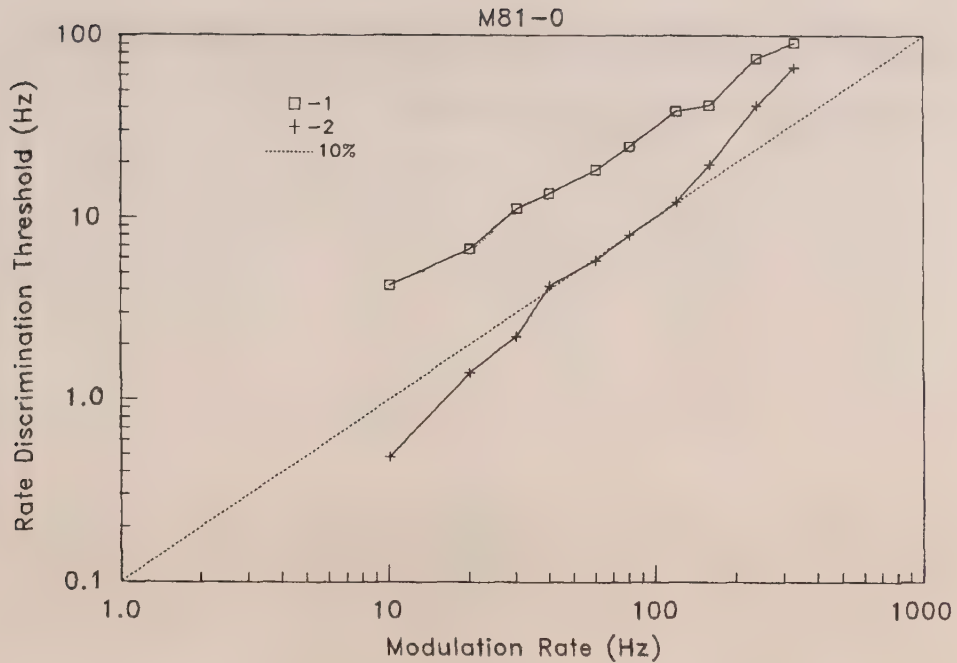


Fig. M81-0. Modulation rate discrimination thresholds in *Chinchilla laniger* (chinchilla) and *Homo sapiens* (human) (Long and Clark, 1984).

- 1- *Chinchilla laniger* - chinchilla
- 2- *Homo sapiens* - human

Reference:

Long, G.R. and Clark, W.W. (1984) Detection of frequency and rate modulation by the chinchilla. *J. Acoust. Soc. Amer.* 75, 1184-1190.

Table M81-0. Modulation rate discrimination thresholds in *Chinchilla laniger* (chinchilla) and *Homo sapiens* (human) (Long and Clark, 1984).

Modulation Rate (Hz)	Modulation Rate Discrimination Threshold (Hz)	
	1	2
10	4.23	0.48
20	6.7	1.4
30	11.1	2.2
40	13.4	4.2
60	18.2	5.8
80	24.4	8
120	38.2	12.1
160	41.2	19.5
240	74.4	41
330	90.7	66

Notes:

Operant conditioning for a food reward using a staircase procedure. Animals were trained to make an observing response, and then terminate the response in the presence of the signal. Amplitude modulated noise (100% modulated, 65 dB SPL, 0.5-10 kHz) was presented continuously. The signal to be detected was a 2 Hz sinusoidal modulation of the modulation rate. Thresholds were defined as the RMS amplitude of rate modulation which was just detectable. Chinchilla data are calculated as period discrimination thresholds in Fig. M82-0. Means: N=3 chinchillas, N=4 humans.

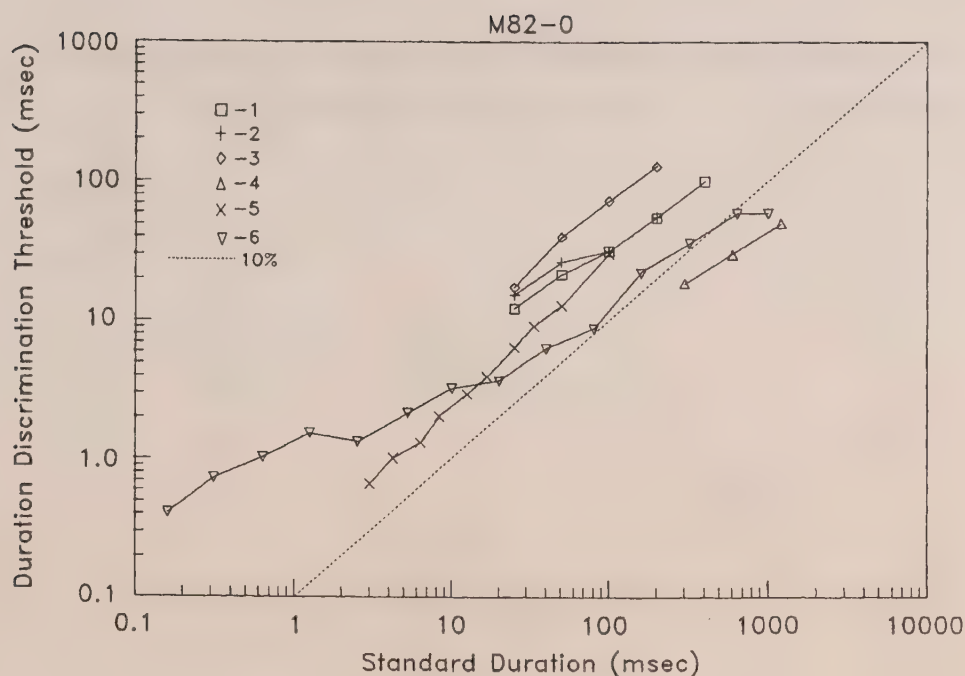


Fig. M82-0. Auditory duration discrimination in several mammal species.

- 1- *Macaca mulatta* - rhesus macaque
- 2- *Cercopithecus aethiops* - vervet monkey
- 3- *Cercopithecus neglectus* - de Brazza monkey
(Sinnott, Owren, and Petersen, 1987)
- 4- *Tursiops truncatus* - bottlenose dolphin (Yunker and Herman, 1974)
- 5- *Chinchilla laniger* - chinchilla (Long and Clark, 1984)
- 6- *Homo sapiens* - human (Abel, 1972)

References:

- Abel, S. (1972) Duration discrimination of noise and tone bursts. *J. Acoust. Soc. Amer.* 51, 1219-1223.
- Long, G.R. and Clark, W.W. (1984) Detection of frequency and rate modulation by the chinchilla. *J. Acoust. Soc. Amer.* 75, 1184-1190.
- Sinnott, J.M., Owren, M.J., and Petersen, M.R. (1987) Auditory duration discrimination in Old World monkeys (*Macaca*, *Cercopithecus*) and humans. *J. Acoust. Soc. Amer.* 82, 465-470.
- Yunker, M.P. and Herman, L.M. (1974) Discrimination of auditory temporal differences by the bottlenose dolphin and by the human. *J. Acoust. Soc. Amer.* 56, 1870-1875.

Table M82-0. Auditory duration discrimination in several mammal species.

Duration (msec)	Duration Discrimination Threshold (msec)					
	1	2	3	4	5	6
0.16						0.4
0.31						0.71
0.63						1
1.25						1.5
2.5						1.3
3					0.65	
4.2					0.99	
5.2						2.1
6.3					1.28	
8.3					1.98	
10						3.2
12.5					2.9	
16.7					3.9	
20						3.6
25	12	15	17		6.3	
33.3						9
40						6.2
50	21	26	39		12.6	
80						8.6
100	31	31	71		29.7	
160						21.5
200	54	55	125			
300				18.3		
320						35.3
400	98					
600				29.4		
640						58
1000						58
1200				49.2		

Notes:

1-3- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained in a go, no-go, "repeating standard AX" procedure. Signals were 2 kHz tone bursts with 10 msec rise/fall times, at 70 dB SPL, repeated at intervals from 750 to 1250 msec. An increase in signal duration was to be detected. Earphones were used. Humans were tested (data not shown here). Means: N=2 macaques, N=1 vervet monkey, and N=1 de Brazza monkey. Thresholds increased slightly at lower SPLs. Data were also obtained for decreases in duration, but this task was very difficult.

4- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to "station" and to go to the left if a "standard" signal duration was presented, and to go right for a longer signal duration. This was a single successive discrimination requiring the animals to remember the standard duration from trial to trial. Signals were 9 and 25 kHz tones at 17 to 19 dB re: 1 dyne cm⁻². The data given were corrected for a response bias. N=1.

5- Same methods and thresholds as in Fig. M81-0. Modulation rate discrimination thresholds were calculated as modulation period (or interval) discrimination thresholds in this figure. Means: N=3.

6- Two-interval, forced-choice procedure using the method of constant stimuli. Signals were a pair of noise bursts (low-pass filtered at 4000 Hz) at 85 dB SPL separated by 500 msec. Means: N=2. Data were also obtained for tones (not shown here).

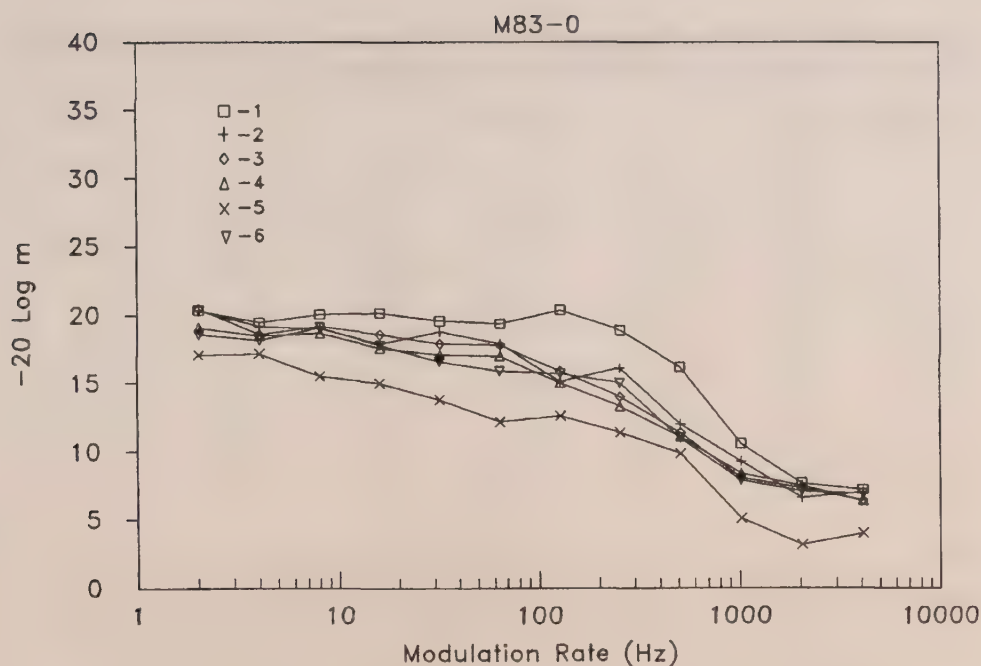


Fig. M83-0. Amplitude modulation detection sensitivity as a function of modulation rate in *Chinchilla laniger* (chinchilla) with high frequency hearing loss.

- 1- Before exposure to noise
- 2- 8 kHz octave band noise exposure
- 3- 4+8 kHz octave band noise exposure
- 4- 2+4+8 kHz octave band noise exposure
- 5- 1+2+4+8 kHz octave band noise exposure
- 6- 1+2+4+8 kHz octave band noise exposure at 23 dB higher noise level

Reference:

Henderson, D., Salvi, R., Pavak, G., and Hamernik, R.P. (1984) Amplitude modulation thresholds in chinchillas with high-frequency hearing loss. *J. Acoust. Soc. Amer.* 75, 1177-1183.

Table M83-0. Amplitude modulation detection sensitivity as a function of modulation rate in *Chinchilla laniger* (chinchilla) with high frequency hearing loss.

Modulation Rate (Hz)	-20 Log m					
	1	2	3	4	5	6
2	20.3	20.3	20.4	19	17	18.5
4	19.4	19.1	18.5	18.4	17.1	18.1
8	20	18.9	19.1	18.6	15.4	19
16	20.1	17.8	18.5	17.5	14.9	17.7
32	19.5	18.7	17.8	17	13.7	16.5
64	19.3	17.8	17.7	16.9	12.1	15.8
128	20.3	15	15.8	14.9	12.5	15.6
256	18.8	16	13.9	13.2	11.3	14.9
512	16.1	11.9	11.3	11	9.8	10.9
1024	10.5	9.2	8	8.3	5	7.8
2048	7.6	6.5	7.2	7.4	3.1	7
4096	7.1	6.9	6.3	6.3	3.9	6.8

Notes:

Instrumental shock-avoidance conditioning using the method of constant stimuli. Animals were restrained over a shock grid, and trained to lift their feet off the grid in order to avoid shock. Signal was continuous wide band noise (20 kHz low pass, 53 dB SPL) that was amplitude modulated sinusoidally. Signal was the addition of modulation to continuous noise for two sec. Humans also tested. Monaural animals. Means: N=3.

The indicated noise exposure conditions are defined as follows. The same individual chinchillas were exposed to four different octave bands of noise, centered on the indicated frequencies, over four weeks. The noise exposures were chosen so that a high frequency hearing loss would occur and spread to lower frequencies as additional exposures were made. The level of each band was 86 to 90 dB SPL.

In the final condition (after exposure to all four noise bands simultaneously), the level of the noise carrier in the amplitude modulated stimulus was raised by 23 dB. The resulting TMTF showed an improvement over the previous function determined after the 8+4+2+1 noise exposure, but did not return to the pre-exposure levels of sensitivity. This suggests that the loss of modulation detection sensitivity is not simply due to an effective reduction in signal level.

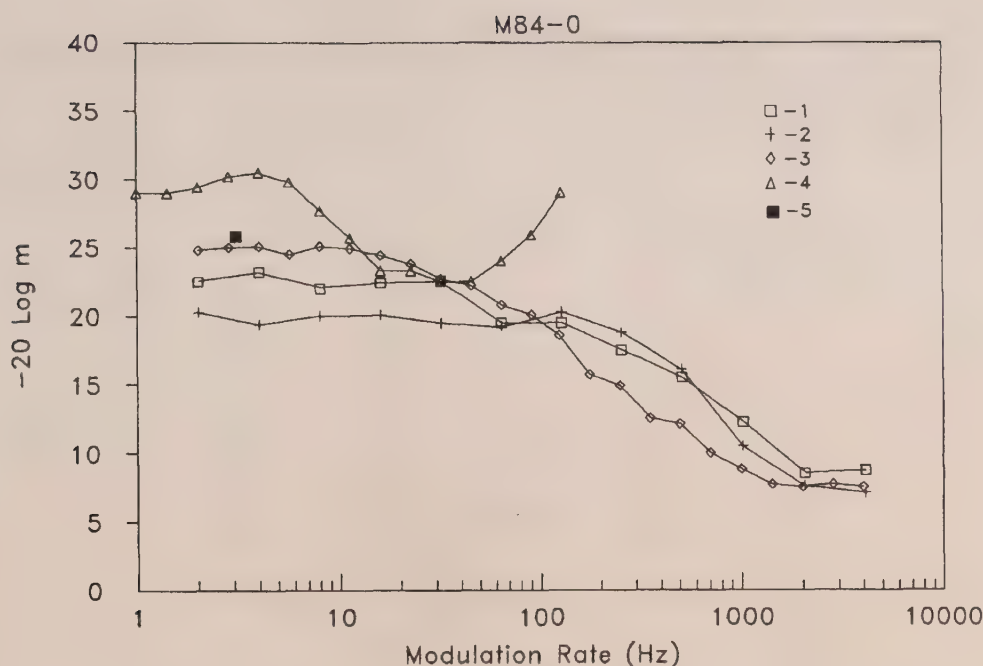


Fig. M84-0. Amplitude modulation detection sensitivity as a function of modulation rate in several mammal species.

- 1- *Chinchilla laniger* - chinchilla (Salvi, Giraudi, Henderson, and Hamernik, 1982)
- 2- *Chinchilla laniger* - chinchilla (Henderson, Salvi, Pavék, and Hamernik, 1984)
- 3- *Homo sapiens* - human (noise) (Viemeister, 1979)
- 4- *Homo sapiens* - human (1 kHz tone) (Viemeister, 1979)
- 5- *Tursiops truncatus ponticus barabasch* - Black Sea bottlenose dolphin (Burdin, Markov, Reznik, Skornvakov, and Chupakov, 1973)

References:

- Burdin, V.I., Markov, V.I., Reznik, A.M., Skornvakov, V.M., and Chupakov, A.G. (1973) Determination of the just noticeable intensity difference for white noise in the Black Sea bottlenose dolphin (*Tursiops truncatus ponticus barabasch*). In K.K. Chapskii and V.E. Sokolov (eds), *Morphology and Ecology of Marine Mammals*. Wiley: New York, pp. 169-173.
- Henderson, D., Salvi, R., Pavék, G., and Hamernik, R.P. (1984) Amplitude modulation thresholds in chinchillas with high-frequency hearing loss. *J. Acoust. Soc. Amer.* 75, 1177-1183.
- Salvi, R.J., Giraudi, D.M., Henderson, D., and Hamernik, R.P. (1982) Detection of sinusoidal amplitude modulated noise by the chinchilla. *J. Acoust. Soc. Amer.* 71, 424-429.
- Viemeister, N.F. (1979) Temporal modulation transfer functions based upon modulation thresholds. *J. Acoust. Soc. Amer.* 66, 1364-1380.

Table M84-0. Amplitude modulation detection sensitivity as a function of modulation rate in several mammal species.

Modulation Rate (Hz)	1	2	-20 Log m 3	4	5
1				29	
1.4				29	
2	22.5	20.3	24.8	29.4	
2.8			25	30.2	
3					26
4	23.2	19.4	25.1	30.5	
5.7			24.5	29.8	
8	22	20	25.1	27.7	
11.3			24.9	25.7	
16	22.4	20.1	24.4	23.3	
22.6			23.8	23.3	
32	22.6	19.5	22.7	22.5	
45.3			22.2	22.5	
64	19.5	19.3	20.8	24	
90.5			20.1	25.9	
125			18.6		
128	19.5	20.3		29	
177			15.7		
250			14.9		
256	17.5	18.8			
354			12.5		
500			12.1		
512	15.5	16.1			
707			10		
1000			8.8		
1024	12.2	10.5			
1414			7.7		
2000			7.5		
2048	8.5	7.6			
2828			7.7		
4000			7.5		
4096	8.7	7.1			

Notes:

1- Instrumental shock-avoidance using constant stimuli. Restrained animals were trained to lift their feet off a grid to avoid shock. Background was continuous wide band noise (20 kHz low pass, 53 dB SPL). Signal was the addition of sinusoidal amplitude modulation for two sec. Humans also tested. Monaural animals. Means: N=4.

Data also obtained with 10 kHz low-pass noise at 72 or 73 dB SPL differed little from those shown here. The half-power point is at 112 Hz, (time constant = 1.4 msec).

2- Same as #1. Means: N=3. See Fig. M83-0 for effects of hearing impairment.

3- Two-interval, forced-choice tracking for about 71% correct. Noise level 40 dB spectrum level at 1 kHz. There is little overall effect on this function of different overall noise levels. Thresholds are smallest for wide band noise, and decline as high frequencies are filtered out. This TMTF has a band-pass shape for gated conditions.

4- Same as #3. Signal was 1 kHz tone at 50 dB SPL. The gain in sensitivity at rates beyond 50 Hz due to detection of spectral energy at the side-band frequencies.

5- Operant conditioning for food reward. Modulation depth at threshold = 5%. Unmodulated noise added to 100% modulated noise to reduce modulation depth. N=1.

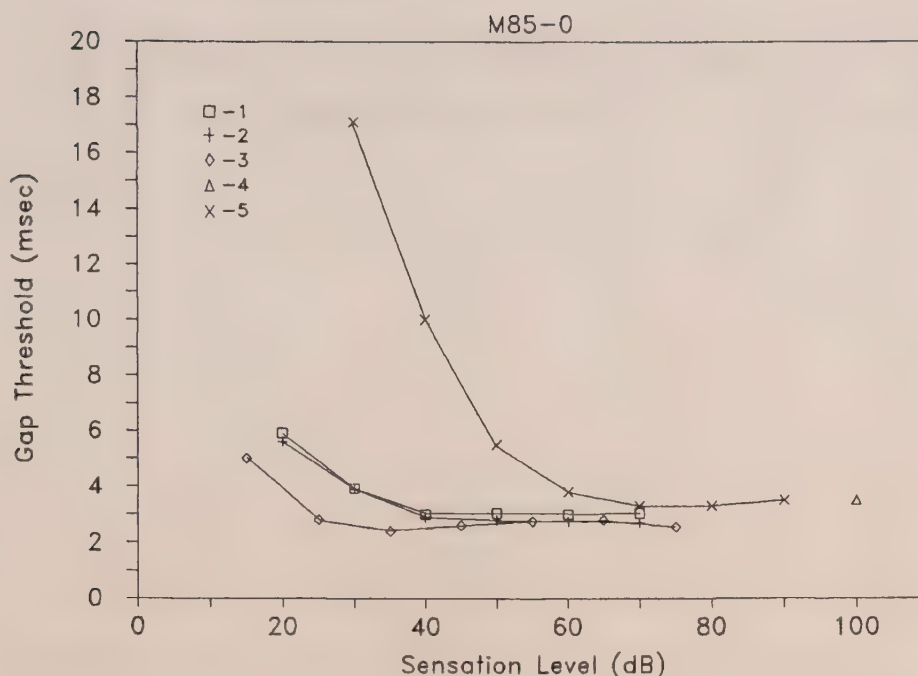


Fig. M85-0. Temporal gap detection thresholds in several mammal species.

- 1- *Chinchilla laniger* - chinchilla (Giraudi, Salvi, Henderson, and Hamernik, 1980)
- 2- *Chinchilla laniger* - chinchilla (Giraudi-Perry, Salvi, and Henderson, 1982)
- 3- *Chinchilla laniger* - chinchilla (Salvi and Arehole, 1985)
- 4- *Rattus norvegicus* - albino rat (Ison, 1982)
- 5- *Homo sapiens* - human (Irwin, Hinchcliffe, and Kemp, 1981)

References:

- Giraudi, D., Salvi, R., Henderson, D., and Hamernik, R. (1980) Gap detection in the chinchilla. *J. Acoust. Soc. Amer.* 68, 802-806.
- Giraudi-Perry, D.M., Salvi, R.J., and Henderson, D. (1982) Gap detection in hearing-impaired chinchillas. *J. Acoust. Soc. Amer.* 72, 1387-1393.
- Irwin, R.J., Hinchcliffe, L.K., and Kemp, S. (1981) temporal acuity in normal and hearing impaired listeners. *Audiol.* 20, 234-243.
- Ison, J.R. (1982) Temporal acuity in auditory function in the rat. *J. Comp. Physiol. Psychol.* 96, 945-954.
- Salvi, R.J., and Arehole, S. (1985) Gap detection in chinchillas with temporary high-frequency hearing loss. *J. Acoust. Soc. Amer.* 77, 1173-1177.

Table M85-0. Temporal gap detection thresholds in several mammal species.

Sensation Level (dB)	Minimum Detectable Gap Duration (msec)				
	1	2	3	4	5
15			5		
20	5.92	5.6			
25			2.8		
30	3.92	3.9			17.1
35			2.4		
40	3	2.9			10
45			2.6		
50	3.05	2.8			5.5
55			2.75		
60	3	2.75			3.8
65			2.8		
70	3.05	2.7			3.3
75			2.55		
80					3.3
90					3.5
100				3.5	

Notes:

1- Instrumental shock-avoidance conditioning using the method of constant stimuli. Animals were restrained over a shock grid, and trained to lift their feet off the grid in order to avoid shock. Signal was continuous wide band noise (10 kHz) with gaps of the indicated durations (10 microsec rise/fall times). Gaps occurred repetitively separated by 750 msec of noise. Monaural animals. Means: N=5. Using noise low-passed at 6 kHz raised thresholds by about 0.4 msec (data not shown here).

2- Same methods as #1 using a tracking procedure. Data were collected on normal monauralized animals (Means: N=5). Data were also collected following exposure to 500 Hz center frequency octave noise band. Long term threshold shifts of 15 dB or less had no effect on gap detection. Threshold shifts of up to 30 dB had effects that were due only to a shift of sensation level. Threshold shifts 30 dB or greater caused longer gap detection thresholds that could not be compensated for by an increase in the SPL of the noise which equalized sensation level.

3- Same methods as #2. Means: N=4. Data were collected for normal monauralized animals, and animals with a noise-induced temporary high frequency hearing loss (shown in Fig. M86-0).

4- Reflex inhibition paradigm using a method of constant stimuli. Animals were presented with continuous 70 dB SPL wide band noise. A startle reflex was elicited by a 20 msec (5 msec rise/fall time) 10 kHz tone at 120 dB SPL. At times, the tone was preceded (190 msec) by a gap in the noise which tended to inhibit or reduce the amplitude of the startle reflex. Data were collected in terms of the extent of reflex inhibition caused by the gap as a function of gap duration. The point plotted here is the gap duration resulting in one half the maximum inhibition observed. The sensation level of the noise is unknown, and plotted at 100 dB SL only for clarity. Means: N=11.

5- Two-interval, two-alternative forced choice using a tracking procedure estimating about 71% correct. Continuous noise in a 500 to 5k Hz band. Gaps had 1 msec rise/fall times. Medians: N=6. Persons with conductive hearing loss showed a loss of sensitivity which could be accounted for by the reduction of sensation level caused by the hearing loss. Persons with a sensorineural hearing loss showed elevated gap thresholds which could not be accounted for by a change in sensation level.

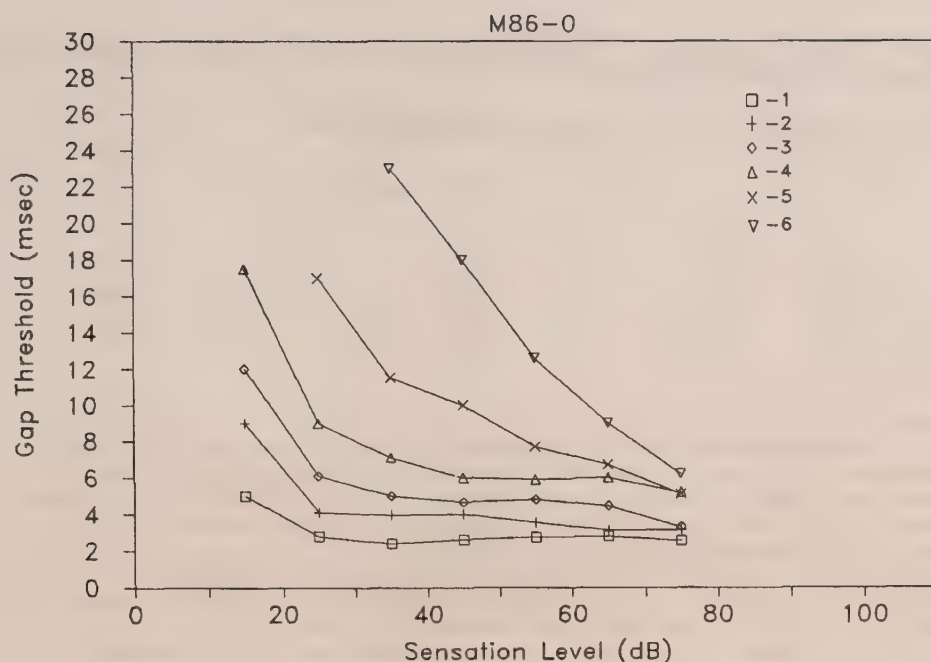


Fig. M86-0. Temporal gap detection thresholds in *Chinchilla laniger* (chinchilla) with temporary high frequency hearing loss.

- 1- Before exposure to noise
- 2- 16 kHz high-pass noise exposure
- 3- 8 kHz high-pass noise exposure
- 4- 4 kHz high-pass noise exposure
- 5- 2 kHz high-pass noise exposure
- 6- 1 kHz high-pass noise exposure

Reference:

Salvi, R.J., and Arehole, S. (1985) Gap detection in chinchillas with temporary high-frequency hearing loss. *J. Acoust. Soc. Amer.* 77, 1173-1177.

Table M86-0. Temporal gap detection thresholds in *Chinchilla laniger* (chinchilla) with temporary high frequency hearing loss.

Sensation Level (dB)	Minimum Detectable Gap (msec)					
	1	2	3	4	5	6
15	5	9	12	17.5		
25	2.8	4.1	6.1	9	17	
35	2.4	3.95	5	7.1	11.5	23
45	2.6	4	4.65	6	10	18
55	2.75	3.55	4.8	5.9	7.7	12.6
65	2.8	3.1	4.45	6	6.7	9

Notes:

Instrumental shock-avoidance conditioning using a tracking method. Animals were restrained over a shock grid, and trained to lift their feet off the grid in order to avoid shock. Signal was continuous wide band noise (10 kHz) with gaps of the indicated durations (10 microsec rise/fall times). Gaps occurred repetitively separated by 750 msec of noise. Monaural animals. Means: N=4.

The same animals were tested under each noise condition, beginning with the 16 kHz condition, and progressing toward the lower high-pass values. Animals were exposed to each condition for from four to 24 days. Exposure noise spectrum level remained constant for all exposure conditions. Exposure noise level was 93 dB SPL between 1 and 20 kHz.

These results show that gap detection thresholds are the lowest when the animal is able to hear the noise components at the highest frequencies.

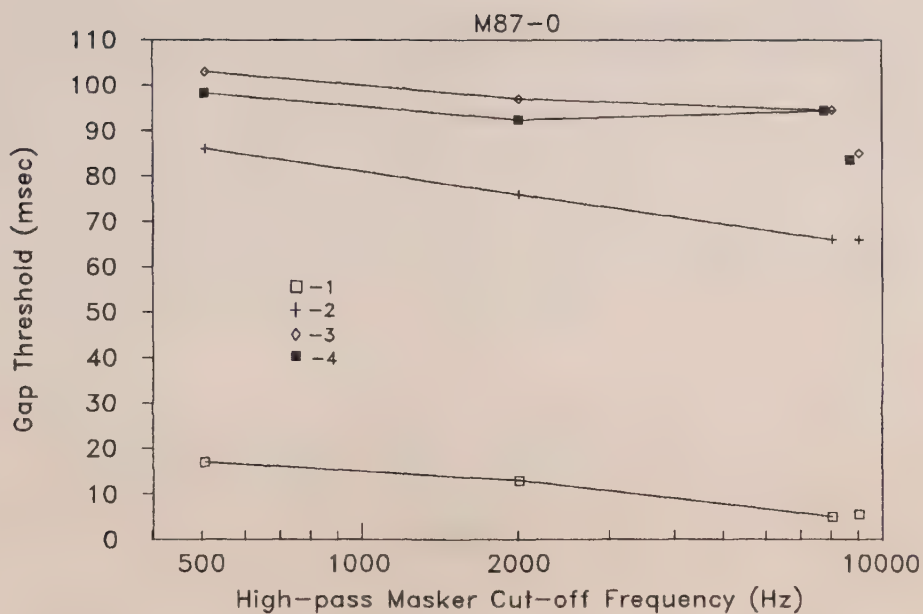


Fig. M87-0. Gap detection thresholds for *Homo sapiens* (human infants and adults) as a function of high-pass masker cut-off frequency.

- 1- Adults
- 2- 12 month-old infants
- 3- 6 month-old infants
- 4- 3 month-old infants

The unconnected points indicate thresholds obtained without additional (masking) noise.

Reference:

Olsho, L.W., and Halpin, C.F. (1987b) Gap detection thresholds of 3-, 6-, and 12-month-old human infants. Association for Research in Otolaryngology. Abstracts of the Mid-winter meeting, p. 91.

Table M87-0. Gap detection thresholds for *Homo sapiens* (human infants and adults) as a function of high-pass masker cut-off frequency.

High-Pass Noise Cut-Off (Hz)	Gap Threshold (msec)			
	1	2	3	4
500	17	86	103	98
2000	13	76	97	93
8000	5	66	94.5	95
No Masker	5.5	66	85	82

Notes:

Operant response for a visual reward using the method of constant stimuli. Infant was rewarded for some response (usually a head-turn) in the presence of a signal with the chance to watch an illuminated motorized toy. An observer decided on any given trial whether the infant responded using whatever criteria the observer could use. The reward to the infant followed the correct detection by the observer. Adults were tested similarly. Signals were gaps in continuous wide band noise (50 dB SPL), occurring twice per sec for 5 sec, delivered to one ear over headphones. When an additional masker noise was used, it was steeply high-pass filtered at the indicated cut-off frequencies. Means: N=10 adults, N=14 3 month-olds, N=13 6 month-olds, N=7 12 month-olds.

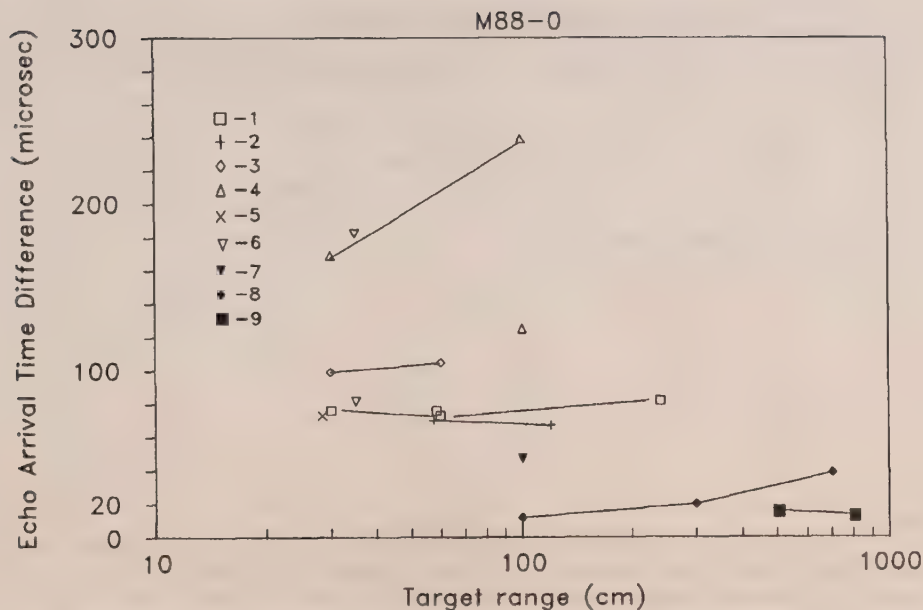


Fig. M88-0. Time difference discrimination thresholds for biosonar echoes.

- 1- *Eptesicus fuscus* - big brown bat. (1) Simmons, 1971. (2) Simmons, 1973
- 2- *Phyllostomus hastus* - greater spear-nosed bat (1) Simmons, 1971. (2) Simmons, 1973
- 3- *Pteronotus suapurensis* - naked-backed bat (Simmons, 1973)
- 4- *Rhinolophus ferrumequinum* - greater horseshoe bat (1) (Simmons, 1973)
(2) Ayrapet'yants and Konstantinov, 1974
- 5- *Tadarida brasiliensis* - a free-tailed bat (Simmons, 1978)
- 6- *Noctilio albiventris* - lesser bulldog bat (Roverud and Grinnell, 1985)
- 7- *Myotis oxygnathus* - a large, little brown bat (Ayrapet'yants and Konstantinov, 1974)
- 8- *Tursiops truncatus* - bottlenose porpoise (Murchison, 1980)
- 9- *Tursiops truncatus* - bottlenose porpoise (Ayrapet'yants and Konstantinov, 1974)

References:

- Ayrapet'yants, E. Sh., and Konstantinov, A.I. (1974) Echolocation in nature (two volumes). An English translation from the Russian of the National Technical Information Service, Springfield, VA, JPRS 63328-1 and -2.
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- Roverud, R., and Grinnell, A. (1985) Discrimination performance and echolocation signal integration requirements for target detection and distance determination in the CF/FM bat, *Noctilio albiventris*. *J. Comp. Physiol.* 156, 447-456.
- Simmons, J.A. (1971) Echolocation in bats: Signal processing of echoes for target range. *Science* 171, 925-928.
- Simmons, J.A. (1973) The resolution of target range by echolocating bats. *J. Acoust. Soc. Amer.* 54, 157-173.
- Simmons, J.A., Lavender, W., Lavender, B., Childs, J., Hulebak, K., Rigden, M., and Woolman, B. (1978) Echolocation by free-tailed bats (*Tadarida*). *J. Comp. Physiol.* 125, 291-299.

Table M88-0. Time difference discrimination thresholds for bats and a porpoise.

Target Range (cm)	Echo Arrival Time Difference Threshold (microsec)								
	1	2	3	4	5	6	7	8	9
30	75.8 ²		99.1	169.1 ¹	72.9				
35						174.9 ¹			
35						81.6 ²			
60	72.9 ¹	70 ¹	104.9						
60		70 ²							
60	75.8 ²								
100				239.1 ¹			67.1	12	
100				124 ²					
120		67 ²							
240	81.6 ²								
300								20	
500									16
700								38.7	
800									13

Notes:

1- (1) Operant conditioning for food reward using the descending method of limits. Animals were trained to discriminate which of two triangular plastic targets (to be detected using biosonar) was closer, by hopping or flying in the direction of the closer target. Some animals blinded to confirm that visual cues were not used.

Differential distance discrimination thresholds (75% correct) were converted here to echo time-of-arrival differences. Means: N=3. (2) Same methods as (1). Means: N=8.

2- (1) Same methods as #1. Means: N=3. (2) Same methods as #1. Means: N=3.

3- Same methods as #1. Means: N=3.

4- (1) Same methods as #1. Means: N=2. (2) These data are reported in the review as if for the first time. Operant conditioning for a food reward using a method of descending limits. Animals were trained to move toward (left or right) the source of the pure tone signal which was closest to the animal. N=4.

5- Same methods as #1. Means: N=2.

6- Operant conditioning for a food reward using a descending method of limits. For sequential distance discrimination (1), animals were trained to crawl out of a crevice and go right for targets presented at 35 cm, and to go left for targets at a greater distance. For simultaneous discrimination (2), targets presented simultaneously (left and right), and the animal was trained to crawl toward the near target. Means: N=2.

7- Same methods as #4(2). N=1-8.

8- Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to "station" and to discriminate between two simultaneously present spheres (using biosonar) by striking a manipulandum on the side (left or right) of the closer of the two spheres. N=1.

9- Classically conditioned galvanic skin reflex using a descending method of limits. See Notes Fig. M32-0, #1. Discrimination of range of 33 mm diam steel balls.

In general, for bats (with the exception of *Rhinolophus*), echo delay discrimination is independent of the absolute echo delay (target range). This is consistent with the notion that range determination is a matter of the bat's auditory system effectively cross-correlating the sound of the emitted biosonar signal with its delayed echo (Simmons, 1971; 1973). Some data for the porpoise have been interpreted differently, since the range thresholds increase with distance (Weber's Law). Murchison (1980) interprets these data in terms of the repetition pitch quality of the emitted and returning sound pulse pairs (See Notes for Figs. F55-0 to F59-0.)

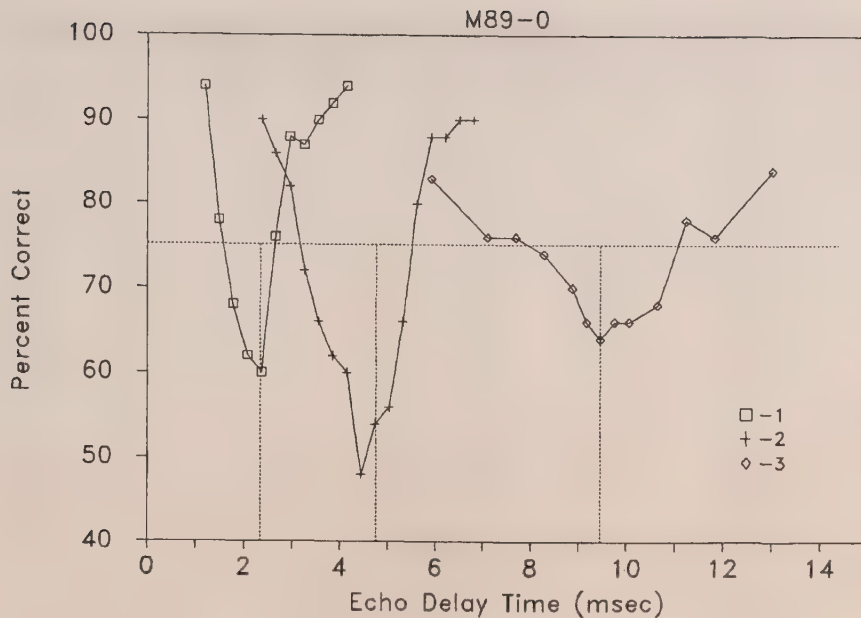


Fig. M89-0. Biosonar echo detection performance as a function of the time delay between a target echo and interfering "clutter" echoes in *Eptesicus fuscus* (big brown bat) (Simmons, Kick, Moffat, Masters, and Kon, 1988).

- 1- Target at 40 cm distance; echo travel time = 2.37 msec
- 2- Target at 80 cm distance; echo travel time = 4.73 msec
- 3- Target at 160 cm distance; echo travel time = 9.47 msec

Reference:

Simmons, J.A., Kick, S.A., Moffat, A.J.M., Masters, W.M., and Kon, D. (1988) Clutter interference along the target range axis in the echolocating bat, *Eptesicus fuscus*. *J. Acoust. Soc. Amer.* (in press).

Table M89-0. Biosonar echo detection performance as a function of the time delay between a target echo and interfering "clutter" echoes in *Eptesicus fuscus* (big brown bat) (Simmons, Kick, Moffat, Masters, and Kon, 1988).

Interfering Clutter Echo Delay (msec)	Percent Correct		
	1	2	3
1.18	94		
1.48	78		
1.78	68		
2.07	62		
2.37	60	90	
2.66	76	86	
2.96	88	82	
3.25	87	72	
3.55	90	66	
3.85	92	62	
4.14	94	60	
4.44		48	
4.73		54	
5.03		56	
5.33		66	
5.62		80	
5.92		88	83
6.21		88	
6.51		90	
6.80		90	
7.1			76
7.69			76
8.28			74
8.88			70
9.17			66
9.47			64
9.76			66
10.06			66
10.65			68
11.24			78
11.83			76
13.02			84

Notes:

Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to use echolocation to decide whether a "target" was on the right or left in the presence of interfering echoes from interfering (clutter) objects near the target. The target was simulated by an electronic system returning a recorded biosonar signal at a time delay appropriate for certain target distances. The clutter was produced by suspending fiberboard rings (10.4 cm outside diameter and 7.7 cm inside diameter) on both sides, centered on the "phantom" target. Target echoes were replicas of the emitted biosonar signals (about 2 to 4 msec in duration, 11 to 18 dB sensation level). The distances of the interfering rings from the animal are expressed here in terms of their echo delay times. N=1.

These data can be viewed as backward and forward masking psychometric functions of signal-masker interval. The "clutter zone" increases with target distance.

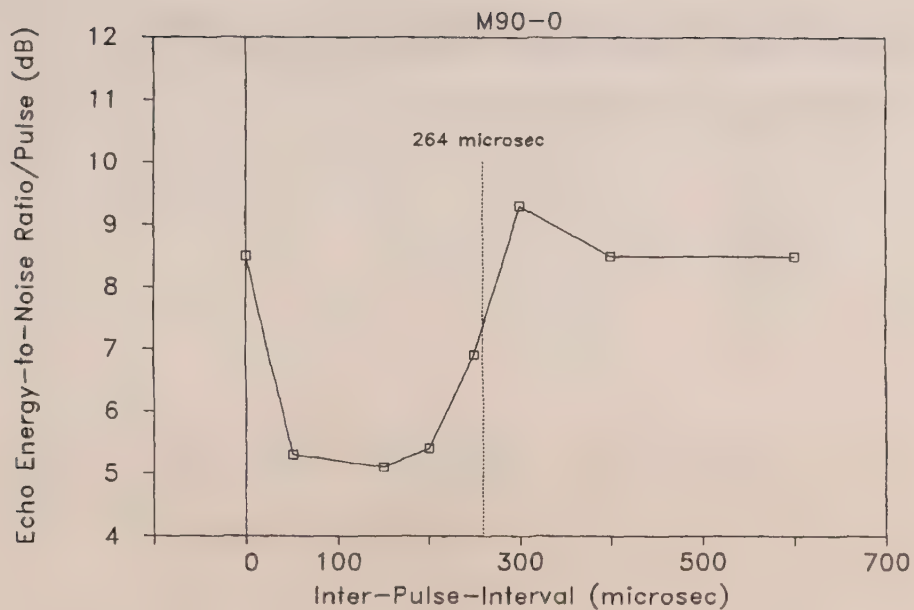


Fig. M90-0. Detection thresholds for biosonar pulses as a function of inter-pulse-interval in *Tursiops truncatus* (bottlenose dolphin) (Au and Moore, 1988).

Reference:

Au, W.L., and Moore, P.W.B. (1988) Detection of complex echoes in noise by an echolocating dolphin. *J. Acoust. Soc. Amer.* 83, 662-668.

Table M90-0. Detection thresholds for biosonar pulses as a function of inter-pulse-interval in *Tursiops truncatus* (bottlenose dolphin) (Au and Moore, 1988).

Inter-Pulse-Interval (microsec)	Pulse Energy-Noise Ratio per Pulse (dB)
0	8.5
50	5.3
150	5.1
200	5.4
250	6.9
300	9.3
400	8.5
600	8.5

Notes:

Operant conditioning for a food reward using the staircase psychophysical procedure. The animal was trained to station, and to echolocate. The emitted biosonar sound pulse was picked up by a hydrophone at 1.9 meters from the animal. The signal was electronically conditioned, mixed with noise (5 to 11 dB above ambient), and then played back to the animal with a time delay appropriate for a target at 20 meters. The signal was either played back as a single pulse (0 microsec inter-pulse-interval condition), or as a double pulse with the indicated inter-pulse-intervals. If the animal detected the returning pulse or pulse pair, it left the station and struck a "signal present" paddle. If the signal was not present, the animal remained stationed for three sec. N=1.

In general, these results show that the addition of a second pulse at short intervals lowers threshold by about 3 dB. For inter-pulse-intervals longer than 250 microsec, threshold returned to the single pulse level. This indicates an integration time for the detection of transients of about 264 microsec (dashed line). This is considerably shorter than the integration times measured using narrow band tone signals (See. Fig. M77-0). Further tests demonstrated that multiple "looks" at the signals in successive integration periods did not improve detectability.

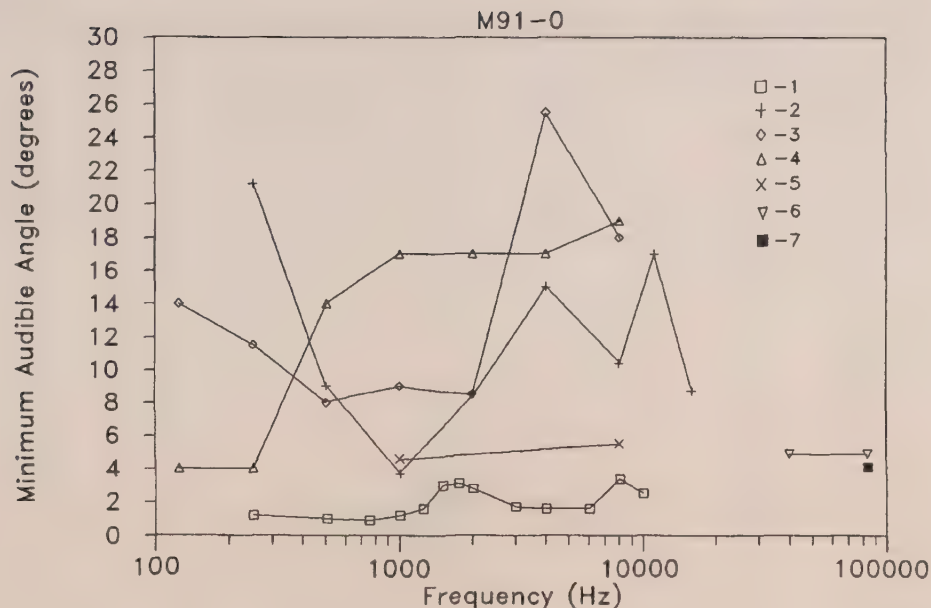


Fig. M91-0. Minimum audible angles for the localization of tones as a function of frequency in several mammals.

- 1- *Homo sapiens* - human (Mills, 1958)
- 2- *Macaca mulatta* - rhesus monkey, and *Macaca nemestrina* - pig-tailed macaque (Brown, Beecher, Moody, and Stebbins, 1978a)
- 3- *Felis catus* - cat (Casseday and Neff, 1973)
- 4- *Elephas maximus* - elephant (Heffner and Heffner, 1982)
- 5- *Phoca vitulina* - harbor seal (Terhune, 1974)
- 6- *Myotis oxygnathus* - a large, little brown bat (Ayrappet'yants and Konstantinov, 1974)
- 7- *Rhinolophus ferrumequinum* - greater horseshoe bat (Ayrappet'yants and Konstantinov, 1974)

References:

- Ayrappet'yants, E.S., and Konstantinov, A.I. (1974) Echolocation in Nature. An English translation of the National Technical Information Service, JPRS #63326-1-2.
- Brown C.H., Beecher M.D., Moody, D.B., and Stebbins W.C. (1978a) Localization of pure tones by Old World monkeys. *J. Acoust. Soc. Amer.* 63, 1484-1492.
- Casseday, J.H., and Neff, W.D. (1973) Localization of pure tones. *J. Acoust. Soc. Amer.* 54, 365-372.
- Heffner, R.S., and Heffner, H.E. (1982) Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Psychol.* 96, 926-944.
- Mills, A.M. (1958) On the minimum audible angle. *J. Acoust. Soc. Amer.* 30, 237-246.
- Terhune, J.M. (1974) Directional hearing in a harbor seal in air and water. *J. Acoust. Soc. Amer.* 56, 1862-1865.

Table M91-0. Minimum audible angles for the localization of tones as a function of frequency in several mammals.

Frequency (Hz)	Minimum Audible Angle (degrees)						
	1	2	3	4	5	6	7
125			14	4			
250	1.2	21.2	11.5	4			
500	1	9	8	14			
750	0.9						
1000	1.2	3.7	9	17	4.6		
1250	1.6						
1500	3						
1750	3.1						
2000	2.8	8.5	8.5	17			
3000	1.7						
4000	1.6	15	25.5	17			
6000	1.6						
8000	3.4	10.4	18	19	5.5		
10000	2.5						
11200		17					
16000		8.7					
40000						4.9	
83500						4.9	4.1

Notes:

1- Two-alternative, forced choice procedure using a method of constant stimuli. Subjects were blindfolded with head fixed in an anechoic chamber. After establishing loudspeaker position defining 0° azimuth, subjects judged whether the second sound pulse of a pair was to the right or left of the first pulse (always at 0°). Signals were one sec long with 70 msec rise-fall times, 50 dB sensation level. Means: N=3.

2- Operant conditioning for a food reward using the method of constant stimuli. Animals seated in an anechoic chamber with the head fixed initiated a trial by holding down a lever (observing response). Signals were 300 msec (25 msec rise-fall time) tone bursts repeated at 1.5 pulses per sec at 40 dB sensation level, from 0° azimuth. Releasing the lever during a period of alternation between the 0° and another speaker displaced in azimuth was rewarded. Medians: N=3.

3- Operant conditioning for a food reward using a method of constant stimuli. Animals trained to approach and open a goal box door behind which sound signal had been given. Signals were 500 msec tones, 100 msec rise/fall times, 50 dB sensation level, repeated five times, once per sec. Humans tested in same apparatus. Means: N=8.

4- Operant conditioning for a liquid reward using a method of constant stimuli. Animals were trained to make an observing response which initiated a 100 msec tone burst (50 msec rise/fall times, 40 dB sensation level) from either a left or right loudspeaker. The animal then made a response with its trunk to the left or right, depending on the sound source location. N=1.

5- Data for localization in air. Operant conditioning for a liquid reward using a method of constant stimuli. Animals made an observing response, and then indicated whether the sound arose from the right or left of center. Signals were 60 dB SPL. N=1.

6- These data are reported in a review paper as if for the first time. Operant conditioning for a food reward using a method of descending limits. Animals trained to move toward (left or right) the source of the 60 dB SPL signal. Means: N=3.

7- Same as #6.

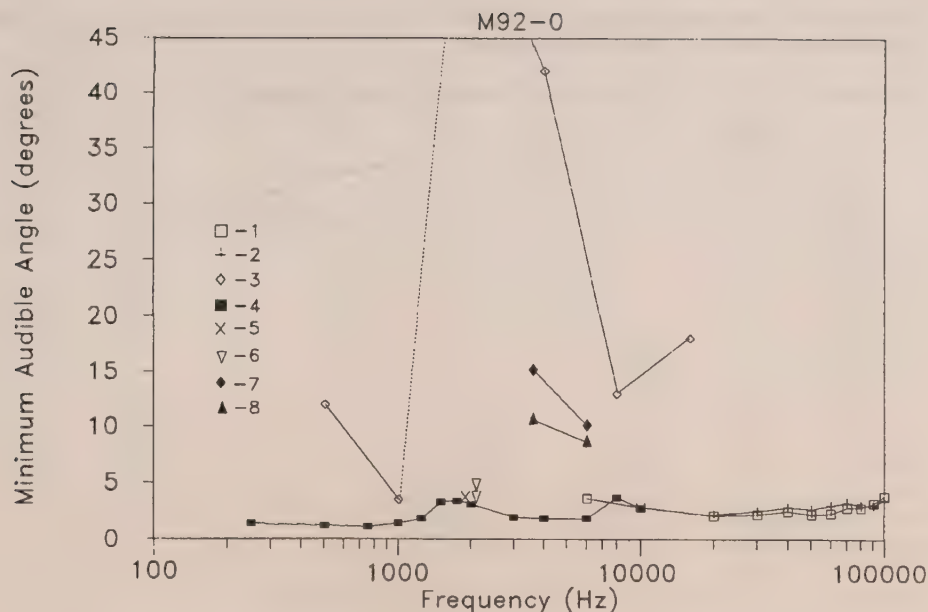


Fig. M92-0. Minimum audible angles for the localization of tones for marine mammals with human MAAs in air for comparison.

- 1- *Tursiops truncatus* - bottlenose porpoise (azimuth) (Renaud and Popper, 1975)
- 2- *Tursiops truncatus* - bottlenose porpoise (elevation) (Renaud and Popper, 1975)
- 3- *Zalophus californianus* - California sea lion (Moore and Au, 1975)
- 4- *Homo sapiens* - human (air) (Mills, 1958)
- 5- *Phocoena phocoena* - harbour porpoise (Andersen, 1970)
- 6- *Phoca vitulina* - harbour seal (in water and in air) (Mohl, 1964)
- 7- *Zalophus californianus* - California sea lion (Gentry, 1967)
- 8- *Phocaena phocaena* - harbour porpoise (Dudok van Heel, 1962)

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- Andersen, S. (1970) Directional hearing in the harbor porpoise, *Phocoena phocoena*. In G. Pilleri (ed) Investigations on Cetacea, Vol. II. Benteli AG: Berne.
- Dudok van Heel, W.H. (1962) Sound and cetacea. *Neth. J. Sea Res.* 1(4), 407-507.
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Table M92-0. Minimum audible angles for the localization of tones for marine mammals with human MAAs in air for comparison.

Frequency (Hz)	Minimum Audible Angle (degrees)					
	1	2	3	5	6	8
500			12		4.8 ^(air)	
1000			3.5			
2000				3	3.1 ^(underwater)	
3500					15	11
4000			42			
6000	3.6				10	7.9
8000			13			
10000	2.8					
16000			18			
20000	2.1	2.2				
30000	2.2	2.5				
40000	2.5	2.8				
50000	2.2	2.7				
60000	2.3	3				
70000	2.8	3.3				
80000	2.8	3				
90000	3.2	3				
100000	3.8	3.5				

Notes:

1-2- Operant conditioning for a food reward using a tracking procedure. The animal stationed and swam to one of two response paddles indicating from which side of midline the sound was emitted. Signals were 3 msec duration tone pulses with 0.25 msec rise/fall times repeated 80 times per sec at at least 40 dB sensation level. Thresholds defined at 70% correct. Vertical localization (elevation) was tested with the same source arrays by training the animal to station effectively on its side. N=1.

3- Operant conditioning for food using method of constant stimuli. Animals stationed, and pushed one response paddle if the signal arose from the source at 0° azimuth, and pressed another paddle for a signal at the left. 20 msec tone pulses with 5 msec r/f times repeated at 30 per sec. MAAs defined for 70% correct performance. N=1.

4- Data tabled in Fig. M91-0, #1. Two-alternative, forced choice procedure using a method of constant stimuli. Subjects were blindfolded with head fixed in an anechoic chamber. After establishing loudspeaker position defining 0° azimuth, subjects judged whether the second sound pulse of a pair was to the right or left of the first pulse (always at 0°). Signals were one sec long with 70 msec rise-fall times, 50 dB sensation level. Means: N=3.

5- Operant conditioning for a food reward using a method of constant stimuli. Animal trained to swim through two hoops and then swim right or left depending on the source location of the sound signal (which was presented only while the animal was between the two hoops). Signal was a 2 kHz tone, about 500 msec in duration, presented at 20 dB re: 1 dyne cm⁻². N=1.

6- Operant conditioning for food reward using the method of constant stimuli. Animals stationed and then indicated which of two speakers (symmetrically placed right and left of midline) had broadcast a tone signal by swimming to the appropriate source. Signals were 580 msec tone bursts at 500 Hz (55 dB SPL in air) and 2 kHz (-7 dB re: 1 dyne cm⁻² in water). N=1.

7- Same as #6. Signals 300-400 msec tones at 4 dB re: 1 dyne cm⁻². N=1.

8- Essentially the same as #5. 670 msec pure tone. N=1.

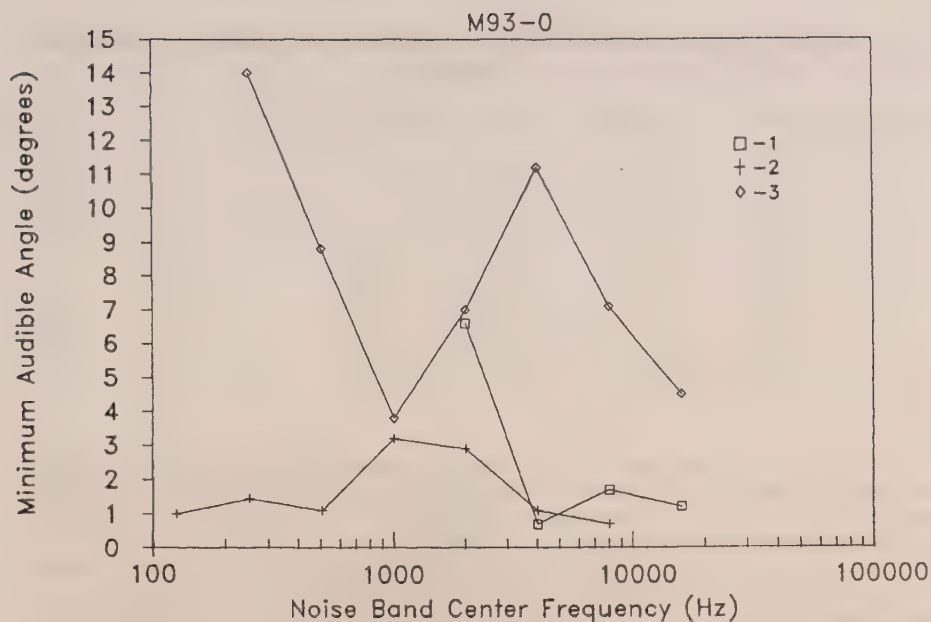


Fig. M93-0. Minimum audible angles for localizing noise bands as a function of noise band center frequency in several mammals.

- 1- *Phoca vitulina* - harbor seal (Terhune, 1974)
- 2- *Elephas maximus* - elephant (Heffner and Heffner, 1982)
- 3- *Macaca mulatta* - rhesus monkey
Macaca nemistrina - pig-tailed macaque
 (Brown, Beecher, Moody, and Stebbins, 1980)

References:

- Brown C.H., Beecher M.D., Moody, D.B., and Stebbins W.C. (1980) Localization of noise bands by Old World monkeys. *J. Acoust. Soc. Amer.* 68, 127-132.
- Heffner, R.S., and Heffner, H.E. (1982) Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Psychol.* 96, 926-944.
- Terhune, J.M. (1974) Directional hearing in a harbor seal in air and water. *J. Acoust. Soc. Amer.* 56, 1862-1865.

Table M93-0. Minimum audible angles for localizing noise bands as a function of noise band center frequency in several mammals.

Center Frequency (Hz)	Minimum Audible Angle (degrees)		
	1	2	3
125		1	
250		1.45	14
500		1.1	8.8
1000		3.2	3.8
2000	6.6	2.9	7
4000	0.7	1.1	11.2
8000	1.7	0.7	7.1
16000	1.2		4.5

Notes:

1- Data for localization in air. Operant conditioning for a liquid reward using a method of constant stimuli. Animals made an observing response, and then indicated whether the sound arose from the right or left of center. Signals were 75 dB SPL, 1/3 octave noise bands. N=1.

2- Operant conditioning for a liquid reward using a method of constant stimuli. Animals were trained to make an observing response which initiated a 100 msec noise burst (band-pass filtered at the indicated frequency with 24 dB/octave roll-offs, 50 msec rise/fall times, 40 dB sensation level) from either a left or right loudspeaker. The animal then made a response with its trunk to the left or right, depending on the sound source location. N=1.

3- Operant conditioning for a food reward using the method of constant stimuli. Animals seated in an anechoic chamber with the head fixed initiated a trial by holding down a lever (observing response). Signals were 300 msec (25 msec rise-fall time) noise bursts (0.36 octave wide, at the indicated center frequency) repeated at 1.5 pulses per sec at 40 dB sensation level, from 0° azimuth. Releasing the lever during a period of alternation between the 0° and another speaker displaced in azimuth was rewarded. Similar data also obtained for noise bands 0.714 octave and 1.39 octave wide (not shown here). The effect of center frequency declines as the noise band widens. Medians: N=3.

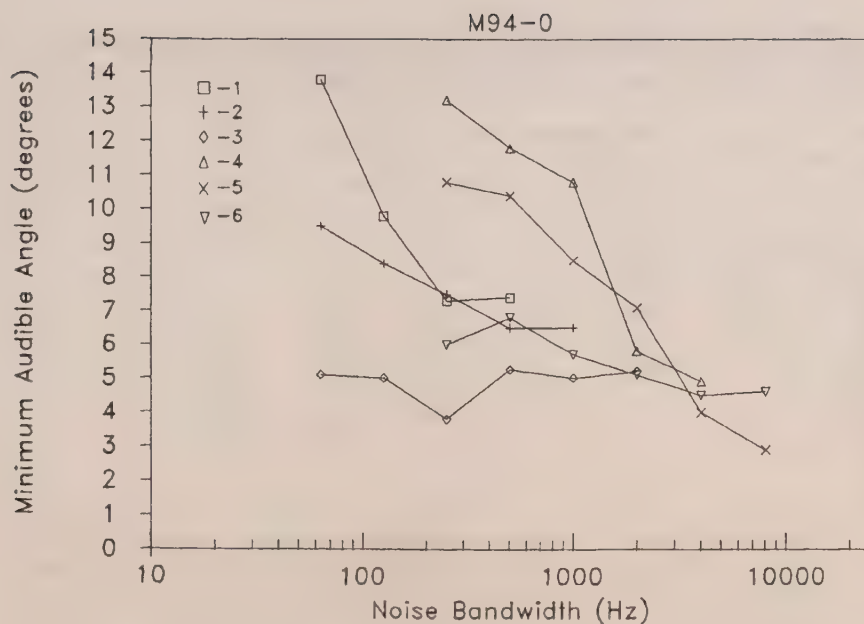


Fig. M94-0. Minimum audible angles localizing noise bands as a function of noise bandwidth in *Macaca mulatta* (rhesus monkey) and *Macaca nemistrina* (pig-tailed macaque) (Brown, Beecher, Moody, and Stebbins, 1980)

- 1- 250 Hz noise center frequency
- 2- 500 Hz
- 3- 1000 Hz
- 4- 4000 Hz
- 5- 8000 Hz
- 6- 16000 Hz

References:

Brown C.H., Beecher M.D., Moody, D.B., and Stebbins W.C. (1980) Localization of noise bands by Old World monkeys. *J. Acoust. Soc. Amer.* 68, 127-132.

Table M94-0. Minimum audible angles localizing noise bands as a function of noise bandwidth in *Macaca mulatta* (rhesus monkey) and *Macaca nemistrina* (pig-tailed macaque) (Brown, Beecher, Moody, and Stebbins, 1980)

Noise Bandwidth (Hz)	Minimum Audible Angle (degrees)					
	1	2	3	4	5	6
63	13.8	9.5	5.1			
125	9.8	8.4	5			
250	7.3	7.5	3.8	13.2	10.8	6
500	7.4	6.5	5.25	11.8	10.4	6.8
1000		6.5	5	10.8	8.5	5.7
2000			5.2	5.8	7.1	5.1
4000				4.9	4	4.5
8000					2.9	4.6

Notes:

Operant conditioning for a food reward using the method of constant stimuli. Animals seated in an anechoic chamber with the head fixed initiated a trial by holding down a lever (observing response). Signals were 300 msec (25 msec rise-fall time) noise bursts at the indicated center frequencies and bandwidths) repeated at 1.5 pulses per sec at 40 dB sensation level, from 0° azimuth. Releasing the lever during a period of alternation between the 0° and another speaker displaced in azimuth was rewarded. Similar data also obtained for noise bands centered at 2000 and 11200 Hz (not shown here). Medians: N=3.

These data show that bandwidth has little effect on the MAA for noise centered at 1000 Hz, and 16000 Hz, while there is a significant bandwidth effect at the other frequencies. One interpretation of this is that noise energy in these two regions leads to optimal localization acuity, and that the improvement with bandwidth for the other center frequencies occurs because energy moves into one of these two frequency regions as the noise band widens.

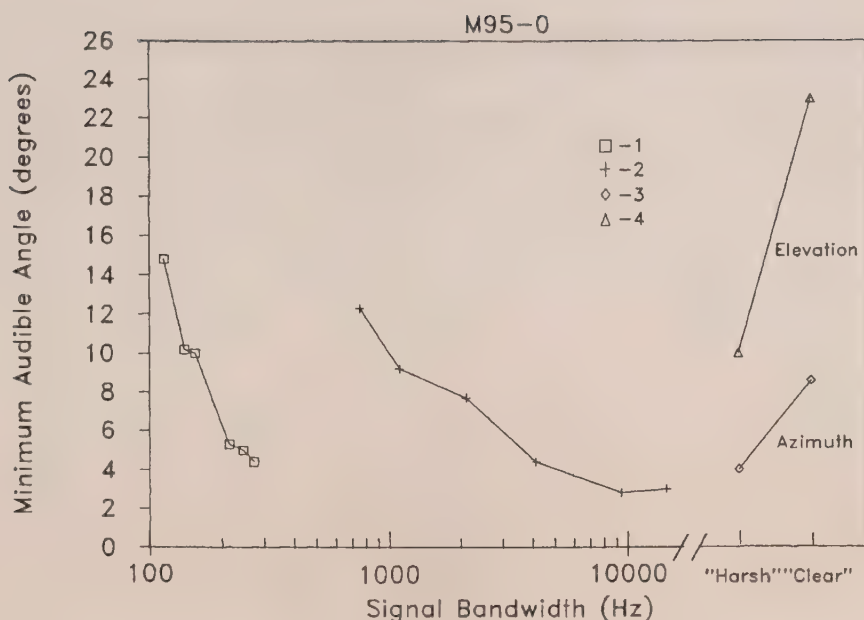


Fig. M95-0. Minimum audible angles for localizing complex signals as a function of signal bandwidth or signal type in *Macaca mulatta* (rhesus monkey) and *Macaca nemestrina* (pig-tailed macaque).

- 1- Vocalizations of Old World monkeys having FM components of indicated bandwidths (Brown, Beecher, Moody, and Stebbins, 1978b)
- 2- Vertical localization low-pass noise of different cut-off frequency
- 3- Azimuthal localization for two different monkey vocalizations
- 4- Vertical localization for two different monkey vocalizations (Brown, Schessler, Moody, and Stebbins, 1982)

References:

- Brown, C.H., Beecher, M.D., Moody, D.B., and Stebbins, W.C. (1978b) Localization of primate calls by Old World monkeys. *Science*, 201, 753-754.
- Brown, C.H., Schessler, T., Moody D., and Stebbins, W. (1982) Vertical and horizontal sound localization in primates. *J. Acoust. Soc. Amer.* 72, 1804-1811.

Table M95-0. Minimum audible angles for localizing complex signals as a function of signal bandwidth or signal type in Old World monkeys.

Bandwidth (Hz) or Vocalization Type	Minimum Audible Angle (degrees)			
	1	2	3	4
115	14.8			
140	10.2			
155	10			
213	5.3			
244	5			
270	4.4			
750		12.3		
1100		9.2		
2100		7.7		
4100		4.4		
9400		2.8		
14400		3		
"Harsh" call			4	10
"Clear" call			8.6	23

Notes:

1- Operant conditioning for a food reward using the method of constant stimuli. Animals seated in an anechoic chamber with the head fixed initiated a trial by holding down a lever (observing response). Releasing the lever during a period of alternation between the "test" (standard) and another speaker displaced in azimuth was rewarded. Signals were different macaque "coo" vocalizations, approximately equal in loudness and duration (100 to 200 msec), but different in the frequency modulation of the fundamental frequency component (in the range of 600-700 Hz, presented at about 50 dB sensation level). Medians: N=3.

2- Same methods as #1. Noise signals were 300 msec duration (25 msec rise/fall times) at 40 dB SPL (A scale). Noise high-pass cut-offs at 125 Hz, and low-pass cut-offs as indicated above. Data for a single animal (M-86) showing best localization performance and with most complete data.

3- Same methods as #1. Azimuthal localization. Signals were two monkey vocalizations known as "harsh" calls (noisy spectrum 200-2000 Hz, 200 msec duration, 40 dB SPL [A scale]) and "clear" calls (harmonic spectrum, 820 Hz fundamental with two successive harmonics, 200 msec duration, 40 dB SPL (A scale).

4- Same as #3. Vertical localization.

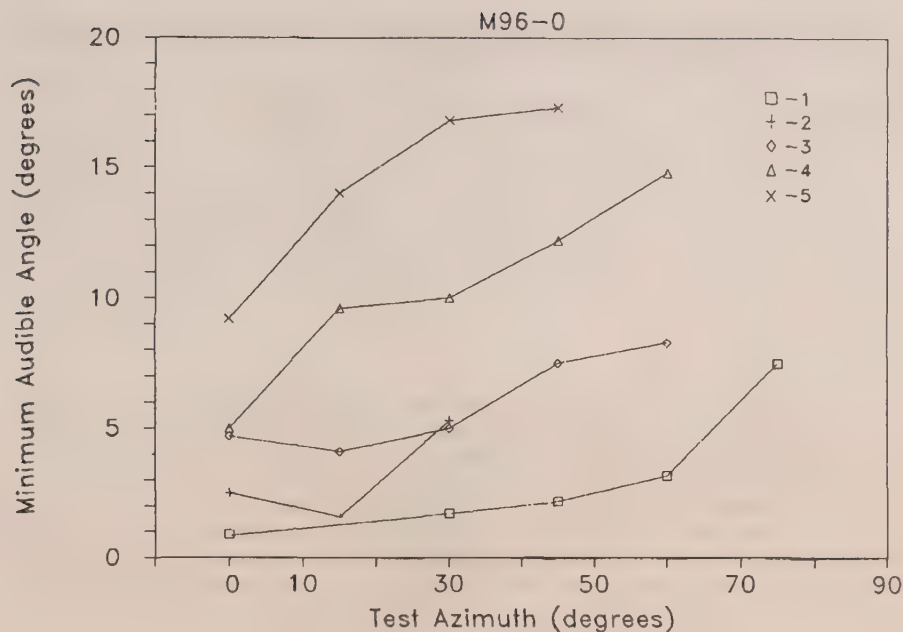


Fig. M96-0. Minimum audible angles for sound localization in several mammals as a function of the azimuth of the standard signal.

- 1- *Homo sapiens* - human (Mills, 1958)
- 2- *Tursiops truncatus* - bottlenose porpoise (Renaud and Popper, 1975)
- 3- 500 Hz signal
- 4- 2000 Hz signal
- 5- 8000 Hz signal
- Macaca nemestrina* - pig-tailed macaque
- Macaca mulatta* - rhesus monkey
- (Brown, Schessler, Moody, and Stebbins, 1982)

References:

- Brown, C.H., Schessler, T., Moody D., and Stebbins, W. (1982) Vertical and horizontal sound localization in primates. *J. Acoust. Soc. Amer.* 72, 1804-1811.
- Mills, A.M. (1958) On the minimum audible angle. *J. Acoust. Soc. Amer.* 30, 237-246.
- Renaud, D.L. and Popper, A.N. (1975) Sound localization by the bottlenose porpoise *Tursiops truncatus*. *J. Exp. Biol.* 63, 569-585.

Table M96-0. Minimum audible angles for sound localization in several mammals as a function of the azimuth of the standard signal.

Test Azimuth (degrees)	Minimum Audible Angle (degrees)				
	1	2	3	4	5
0	0.9	2.5	4.7	5	9.2
15		1.6	4.1	9.6	14
30	1.7	5.3	5	10	16.8
45	2.2		7.5	12.2	17.3
60	3.2		8.3	14.8	
75	7.5				

Notes:

1- Two-alternative, forced choice procedure using a method of constant stimuli. Subjects were blindfolded with head fixed in an anechoic chamber. Subjects judged whether the second sound pulse of a pair was to the right or left of the first pulse positioned at the indicated "test" azimuth. Signals were one sec long 1000 Hz tone bursts with 70 msec rise-fall times, 50 dB sensation level. Means: N=3.

2- Operant conditioning for a food reward using a tracking procedure. The animal stationed and swam to one of two response paddles indicating from which side of midline the sound was emitted. Signal was 3 msec duration, 40 kHz tone pulses with 0.25 msec rise/fall times repeated 80 times per sec at at least 40 dB sensation level. Thresholds defined at 70% correct. Data for test sources to the left and right of 0° azimuth were collapsed. N=1.

3-5- Operant conditioning for a food reward using the method of constant stimuli. Animals seated in an anechoic chamber with the head fixed initiated a trial by holding down a lever (observing response). Signals were 300 msec (25 msec rise-fall time) tone bursts repeated at 1.5 pulses per sec at 40 dB sensation level, from the indicated azimuths. Releasing the lever during a period of alternation between the "test standard" and another speaker displaced in azimuth was rewarded. Medians: N=3.

- 3- 500 Hz signal
- 4- 2000 Hz signal
- 5- 8000 Hz signal

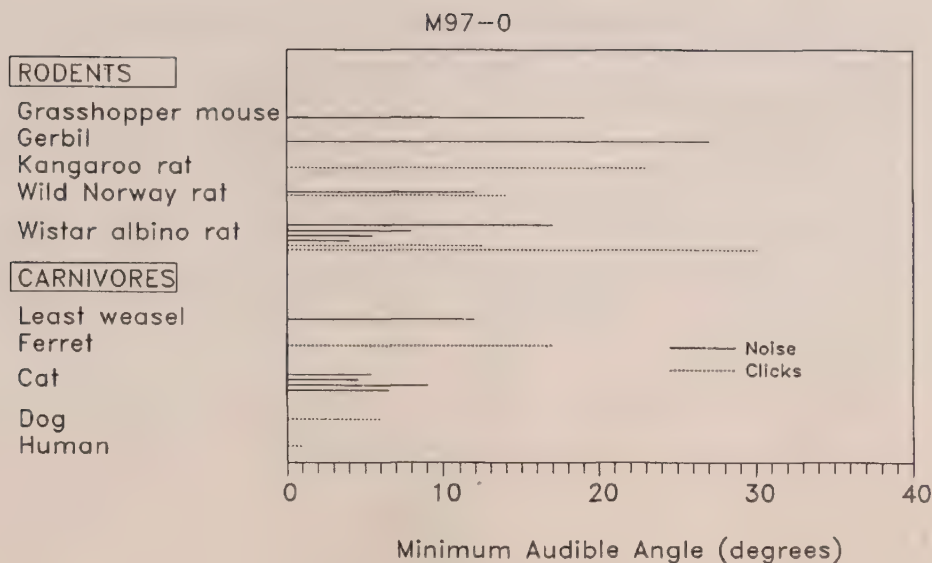


Fig. M97-0. Minimum audible angles (MAA, degrees) for complex signals in several mammals arranged in order of increasing head width.

Rodents

- 1- *Onychomys leucogaster* - grasshopper mouse (Heffner and Heffner, 1988a)
- 2- *Meriones unguiculatus* - gerbil (Heffner and Heffner, 1988b)
- 3- *Dipodomys merriami* - kangaroo rat (Heffner and Masterton, 1980)
- 4- *Rattus norvegicus* - wild Norway rat (Heffner and Heffner, 1985d)
- 5- *Rattus norvegicus* - Wistar albino rat
 - A: (Kelly and Judge, 1985)
 - B: (Kelly, 1980)
 - C: (Kavanagh and Kelly, 1986)
 - D: (Kelly and Glazier, 1978)

Carnivores (terrestrial)

- 6- *Mustela nivalis* - least weasel (Heffner and Heffner, 1987)
- 7- *Mustela putorius* - ferret (Kavanagh and Kelly, 1987)
- 8- *Felis catus* - cat
 - A: (Casseday and Neff, 1975)
 - B: (Moore, Casseday and Neff, 1974)
 - C: (Strominger, 1969)
 - D: (Strominger and Oesterreich, 1970)
- 9- *Canis canis* - dog (Heffner, 1976)
- 10- *Homo sapiens* - human (Heffner and Heffner, 1984)

References:

Due to space limitations, complete references are listed only in the final bibliography.

Table M97-0. MAA (in degrees) for complex signals in several mammals.

<u>Rodents</u>	MAA	SIGNAL TYPE
1- Grasshopper mouse	19	100 msec noise burst
2- Gerbil	27	100 msec noise burst
3- Kangaroo rat	23	single click or train of clicks
4- Wild Norway rat	12	100 msec noise burst
	14	single click
5-(A) Albino rat (Wistar)	17	low frequency filtered noise band
	8	high frequency filtered noise band
5-(B) Albino rat (Wistar)	5.5	low frequency filtered noise band
	4	high frequency filtered noise band
5-(C) Albino rat	12.5	single click
5-(D) Albino rat	30	train of clicks
<u>Carnivores</u>		
6- Least weasel	12	100 msec noise burst
7- Ferret	17	single click
8-(A) Cat	5.4	500 msec noise bursts
8-(B) Cat	4.5	buzzer
8-(C) Cat	9	buzzer
8-(D) Cat	6.6	buzzer
9- Dog	6	clicks
10- Human	0.8	clicks

Notes:

- 1- Instrumental shock avoidance using method of constant stimuli. Successive discrimination between left (warning) and right (neutral) speakers. Signals were single 100 msec noise bursts. Thresholds defined at 0.5 suppression ratio. Medians: N=3.
- 2- Operant conditioning for a food reward using a method of constant stimuli. Animals trained to make an observing response, and then go right or left depending on the location of the sound source. 100 msec noise bursts. Means: N=7.
- 3- Operant conditioning for food using method of constant stimuli. Animals made an observing response, and then to go right or left depending on the location of the sound source. Click train at 2/sec, or a single click gave nearly the same threshold. N=1.
- 4- Same methods as #1. Means: N=3.
- 5- (A) Operant conditioning for a water reward. Animals trained to move to the center of an arena and make an observing response, and then to go to the speaker location which had broadcast a single 80 msec noise burst (20 msec rise/fall times). Two noise stimuli were used: a "low" frequency noise band (bandpass centered on 2 kHz) and a "high" band (bandpass centered on 32 kHz). 40 dB sensation level. N=2.
- 5- (B) Same methods and signals as in #5(A). Medians: N=3.
- 5- (C) Same methods as #5(A). Single click at 58 dB SPL. 75% correct. Mean: N=2.
- 5- (D) Classically conditioned suppression of licking. Clicks 1/sec. Means: N=5.
- 6- Same methods as #1. 100 msec noise burst. N=2.
- 7- Same methods as #5. Single click stimulus.
- 8- (A) Operant conditioning for a food reward using a method of constant stimuli. Animals trained to approach the door behind which a noise signal (500 msec burst at 60 dB SPL, between 100 and 12000 Hz, 100 msec rise/fall times) had been sounded. N=8.
- 8- (B) Same method as #8(A). Signal a 500 msec, 6V buzzer.
- 8- (C) Same methods and signals as #8(B). Means: N=8.
- 8- (D) Same methods and signals as #8(B). Means: N=4.
- 9- Single clicks
- 10- Subjects were to decide whether a click stimulus arose from speakers to the left or right of midline in the same apparatus used to test horses. Means: N=2.

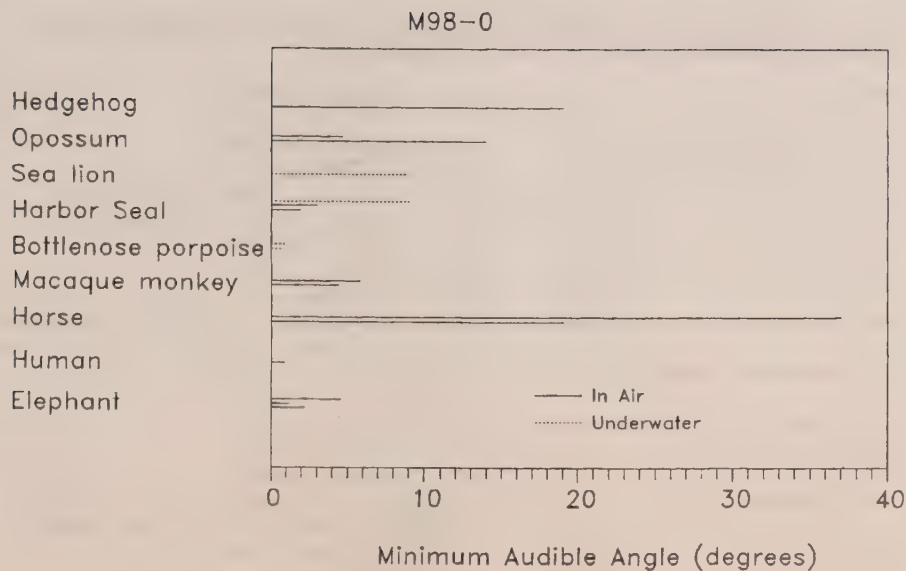


Fig. M98-0. Minimum audible angles (MAA, degrees) for complex signals in several mammals arranged in order of increasing head width.

- 1- *Paraechinus hypomelas* - hedgehog (Chambers, 1971)
- 2- *Didelphis virginiana* - opossum (Ravizza and Masterton, 1975)
- 3- *Zalophus californianus* - sea lion (Moore, 1975)
- 4- *Phoca vitulina* - harbor seal (Terhune, 1974)
- 5- *Tursiops truncatus* - bottlenose porpoise (Renaud and Popper, 1975)
- 6- *Macaca mulatta* - macaque monkey (Heffner and Masterton, 1978)
- 7- *Homo sapiens* - human (Heffner and Heffner, 1984)
- 8- *Equus caballus* - horse (Heffner and Heffner, 1984)
- 9- *Elephas maximus* - elephant (Heffner and Heffner, 1982)

References:

Due to space limitations, complete references are listed only in the final bibliography.

Table M98-0. Minimum audible angles (MAA, degrees) for complex signals in several mammals arranged in order of increasing head width.

SPECIES	MAA	SIGNAL TYPE
1- Hedgehog	19	single click
2- Opossum	4.6	noise burst (azimuth)
	14	noise burst (elevation)
3- Sea lion	8.8	click train (underwater)
4- Harbor seal	9	click (underwater)
	3	click (in air)
	2	wide band noise burst (in air)
5- Bottlenose porpoise	0.9	500 msec click train (azimuth)
	0.7	500 msec click train (elevation)
6- Macaque monkey	5.8	single click
	4.4	click train
7- Human	0.8	click
8- Horse	37	click
	19	noise burst
9- Elephant	4.5	single click
	1.2	0.1 msec rise time noise
	2.2	50 msec rise time noise

Notes:

1- Operant conditioning for water using method of constants. Animals trained to approach the speaker which had emitted the "high intensity" click. Thresholds for 75% correct. For tone pips, performance improves above 8 kHz and at lower frequencies with more rapid rise-times. Means: N=3.

2- Classical conditioned suppression of an ongoing licking response using method of constants. Signal: 100 msec noise at 50 dB SPL. N=2 for azimuth, N=1 elevation.

3- Operant conditioning for food using a method of constant stimuli. Animals stationed and pushed one of two response paddles depending on the source location (0° azimuth, or to the left). 30 clicks/sec for 2.5 sec at 41 dB re: 1 dyne cm⁻². N=1.

4- Operant conditioning for food using a method of constant stimuli. Animals made an observing response and then two different discreet responses depending on the sound source location (right or left of midline). Click was repeated 30 times per sec at 130 dB re: 1 microPa underwater, 80 dB SPL in air. Wide band noise at 75 dB SPL. N=1.

5- Operant conditioning for a food reward using a tracking procedure. The animal stationed and swam to one of two response paddles indicating from which side of midline the sound was emitted. Signals were a 500 msec train of clicks at 300 per sec. Thresholds defined at 70% correct. Vertical localization (elevation) was tested with the same source arrays by training the animal to station effectively on its side. N=1.

6- Operant conditioning for food using a method of constant stimuli. Animals trained to press a lever on the right or left, indicating the side of midline of the source. Clicks at least 40 dB SL. Data from conditioned suppression were similar. Number of clicks had no effect on performance. Auditory cortex lesions primarily affected performance on some tasks (primarily at high frequencies). Means: N=6.

7- Subjects were to decide whether a click stimulus arose from speakers to the left or right of midline in the same apparatus used to test horses (#8). Means: N=2.

8- Operant conditioning for a food reward using a method of constant stimuli. Animals were trained to make an observing response and to make two different discreet responses depending on whether the sound arose from the right or left of midline. Both a single click and a 100 msec wide band noise served as signals. Threshold defined in terms of 75% correct performance. Median: N=3.

9- Same as #8. Single clicks and wide band noise with 0.1 and 50 msec r/f times.

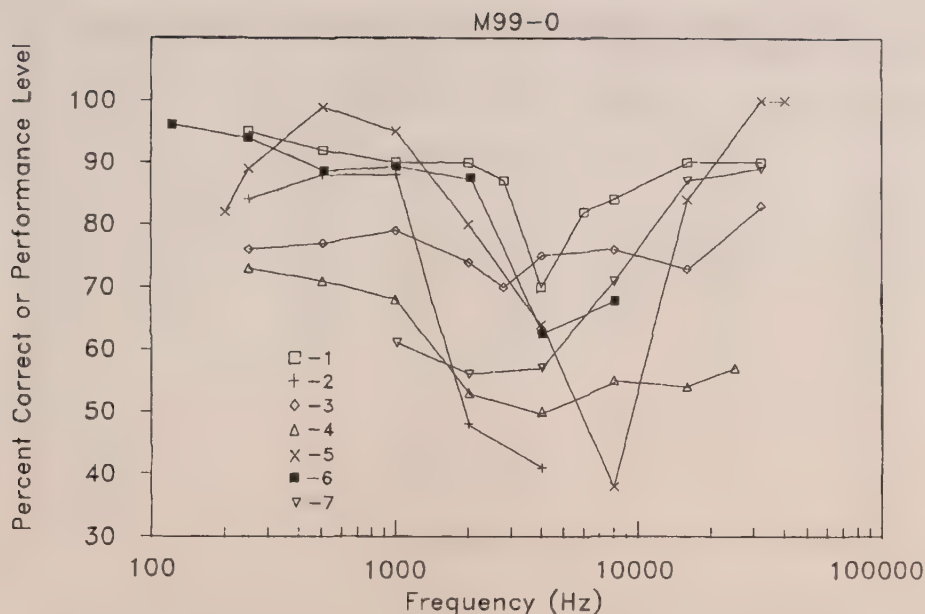


Fig. M99-0. Sound localization performance in screening tests in several mammals.

- 1- *Dipodomys merriami* - kangaroo rat (Heffner and Masterton, 1980)
- 2- *Zalophus californianus* - California sea lion (Moore, 1975)
- 3- *Meriones unguiculatus* - gerbil (Heffner and Heffner, 1988a)
- 4- *Equus caballus* - horse (Heffner and Heffner, 1986)
- 5- *Mustela nivalis* - least weasel (Heffner and Heffner, 1987)
- 6- *Elephas maximus* - Indian elephant (Heffner and Heffner, 1982)
- 7- *Paraechinus hypomelas* - hedgehog (Masterton, Thompson, Bechtold, and RoBards, 1975)

References:

- Heffner, H., and Masterton, R. (1980) Hearing in glires: Domestic rabbit, cotton rat, feral house mouse and kangaroo rat. *J. Acoust. Soc. Amer.*, 1980, 68, 1584.
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- Moore, P.W.B. (1975) Underwater localization of click and pulsed pure-tone signals by California sea lion (*Zalophus californianus*). *J. Acoust. Soc. Amer.* 57, 406-410.

Table M99-0. Sound localization performance in screening tests as a function of signal frequency in several mammals.

Frequency (Hz)	Percent Correct or Performance Level						
	1	2	3	4	5	6	7
125						96	
200					82		
250	95	84	76	73	89	94	
500	92	88	77	71	99	88	
1000	90	88	79	68	95	89	61
2000	90	48	74	53	80	87	56
2800	87		70				
4000	70	41	75	50	64	63	57
6000	82						
8000	84		76	55	38	68	71
16000	90		73	54	84		87
25000				57			
32000	90		83		100		89
40000					100		

Notes:

1- Operant conditioning for a food reward using a method of constant stimuli. Animals trained to make an observing response, and then go right or left depending on the location of the sound source. Sources separated by 60° across midline. Data similar for single click and for two per sec click train. Percent correct. N=1.

2- Underwater localization. Operant conditioning for a food reward. Animals trained to station, and to push one response paddle if the signal arose from the source at 0° azimuth, and to press another paddle if the signal arose from a source fixed 20° to the left. Signals were 20 msec tone bursts with 5 msec rise/fall times, at about 137 dB re: 1 microPa. Percent correct. N=1.

3- Same methods as #1. 100 msec noise burst. Percent correct. Medians: N=4.

4- Operant conditioning for a food reward. Animals were trained to make an observing response and to make two different discrete responses depending on whether the sound arose from the right or left of midline. Sources separated by 60°. Signals 100 msec tone bursts with 50 msec rise/fall times, at 50 dB sensation level. Percent correct. 4 dB random variation in signal level. The authors state that an interaural phase cue is ambiguous in this task at about 1500 Hz. Similar data also collected in an avoidance task (not shown here). Medians: N=3.

5- Instrumental shock avoidance (breaking contact with a licking spout). Successive discrimination between left (warning) and right (neutral) speakers separated by 60°. 100 msec tone signals with 50 msec rise/fall times at 50 dB sensation level. Performance defined as a licking suppression ratio where 100 indicates perfect lick suppression, and 30 is the suppression value expected by chance during discrimination failure. Interaural phase cue is ambiguous in this task at about 13000 Hz. Means: N=2.

6- Operant conditioning for food reward. Animals made an observing response which initiated tone burst signals (100 msec, 50 msec rise/fall times, 40 dB sensation level) from one of two sources separated across the midline by 60°. Interaural phase cue is ambiguous in this task at about 300 Hz and above. Percent correct. N=1.

7- Operant conditioning for water. An observing response initiated a signal (60 msec, 40 msec rise/fall times, at 40 dB sensation level) from one of two sources. Moving to the source that had produced the signal was rewarded. Interaural phase cue ambiguous above 2 kHz. Means: N=2.

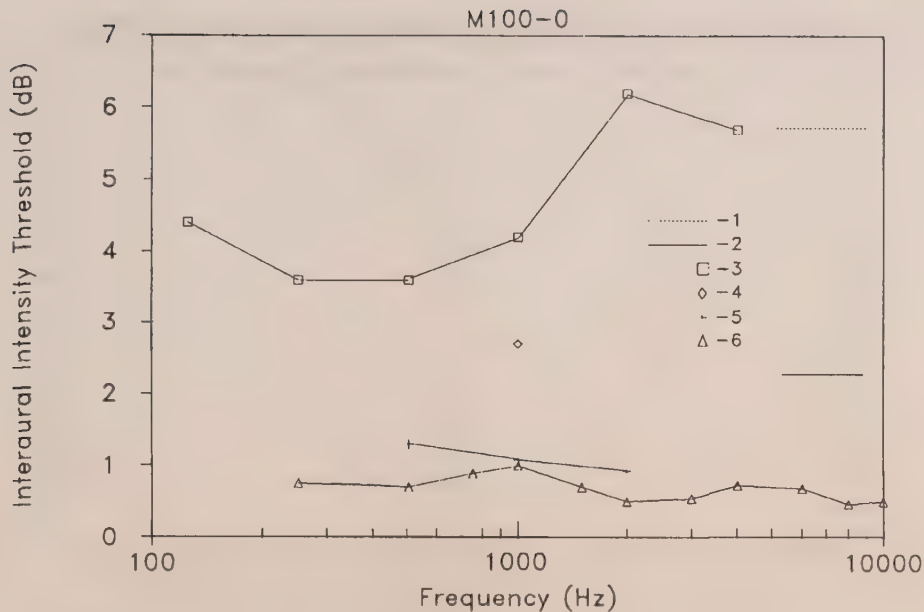


Fig. M100-0. Interaural intensity discrimination thresholds as a function of frequency in several mammals.

- 1- *Samiri sciureus* - squirrel monkey (Don and Starr, 1972)
- 2- *Macaca mulatta* - rhesus monkey (Heffner and Masterton, 1978)
- 3- *Macaca nemistrina* - pig-tailed macaque (Houben and Gourevitch, 1979)
- 4- *Macaca mulatta* - rhesus monkey (Wegener, 1974)
- 5- *Felis catus* - cat (Wakeford and Robinson, 1974b)
- 6- *Homo sapiens* - human (Mills, 1960)

References:

- Don, M., and Starr, A. (1972) Lateralization performance of squirrel monkey (*Samiri sciureus*) to binaural click signals. *J. Neurophysiol.* 35, 493-500.
- Heffner, H. and Masterton, B. (1978) Contribution of auditory cortex to hearing in the monkey (*Macaca mulatta*). In D.J. Chivers, and J. Herbert (eds), *Recent Advances in Primatology*, Vol I. Academic Press: New York, pp. 735-754.
- Houben, D., and Gourevitch, G. (1979) Auditory lateralization in monkeys: An examination of two cues serving directional hearing. *J. Acoust. Soc. Amer.* 66, 1057-1063.
- Mills, A.W. (1960) Lateralization of high frequency tones. *J. Acoust. Soc. Amer.* 32, 132-134.
- Wakeford, O.S., and Robinson, D.E. (1974b) Lateralization of tonal stimuli by the cat. *J. Acoust. Soc. Amer.* 55, 649-652.
- Wegener, J.G. (1974) Interaural intensity and phase angle discrimination by rhesus monkeys. *J. Speech and Hear. Res.* 17, 638-655

Table M100-0. Interaural intensity discrimination as a function of frequency.

Frequency (Hz)	Interaural Intensity Discrimination Threshold (dB)					
	1	2	3	4	5	6
click	5.7	2.25				
125			4.4			
250			3.6			0.75
500			3.6		1.3	0.7
750						0.89
1000			4.2	2.7	1.1	1
1500						0.7
2000			6.2		0.93	0.5
3000						0.54
4000			5.7			0.72
6000						0.68
8000			7.1			0.46
10000						0.5

Notes:

1- Operant conditioning for food using method of constant stimuli. Animals trained to pull a lever on the right or left depending on which ear received most intense signal (32 clicks/sec, about 60 dB above the experimenter's threshold) through earphones. Data for one animal at 10 dB lower level showed a 9 dB higher threshold. Data also obtained on the percent of responses to the right lever as a function of interaural intensity difference (not shown). Thresholds for 85% correct. Means: N=3.

2- Operant conditioning for food using a method of constant stimuli. Animals trained to press a lever on the right or left, indicating the side of midline of the more intense signal. Clicks at least 40 dB SL. N=1.

3- Operant conditioning for food using method of constant stimuli. Animals made an observing response, initiating a trial. Two tone bursts presented binaurally through earphones, 250 msec in duration, separated by 250 msec of silence (10 msec rise/fall times). One ear received identical tone bursts in each interval (60 dB SPL), while for the other ear the second burst was attenuated relative to the first. Means: N=3.

4- Operant conditioning for food reward using method of constant stimuli. Animals trained to press a key to the right for signals more intense in the right ear, and to press the left key for intense signals to the left ear. Earphones held in place with a helmet. Signals were 1000 Hz tone bursts, 500 msec in duration, 3 msec rise-fall times, at 40 dB SPL, separated by 500 msec of silence. 75% correct. Means: N=9.

5- Instrumental shock avoidance using the method of constant stimuli. Animals entered one arm of a triple grill box and then entered one of the other two arms. Signals were 500 msec tone bursts at 70 dB SPL with 50 msec rise/fall times presented through insert earphones held in place with a leather helmet. Animals were presented with repeating 500 msec bursts (separated by 1.17 sec of silence) with a particular interaural disparity in intensity. The discriminative stimulus was a reversal of the binaural disparity across the ears. Threshold defined for P(C)=0.8. Medians: N=3.

6- Subjects listened to pairs of tone bursts (1 sec in duration, separated by 1 sec, 20 msec rise/fall times, at 50 dB sensation level), and indicated whether the second appeared to be lateralized to the right or left of the first. The first always appeared centered, and the interaural intensity disparity of the second burst was manipulated. Proportion of stimuli judged "right" was plotted as a function of interaural intensity difference, and the threshold defined as half the intensity difference between the 25% and 75% points. Medians: N=5.

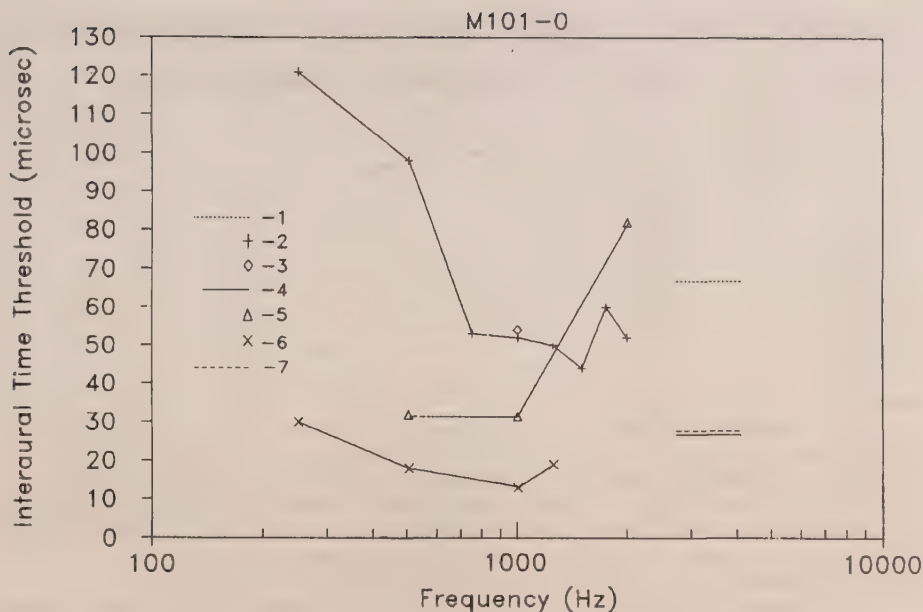


Fig. M101-0. Interaural time discrimination thresholds as a function of frequency.

- 1- *Samiri sciureus* - squirrel monkey (click) (Don and Starr, 1972)
- 2- *Macaca nemestrina* - pig-tailed macaque (Houben and Gourevitch, 1979)
- 3- *Macaca mulatta* - rhesus monkey (Wegener, 1974)
- 4- *Macaca mulatta* - rhesus monkey (click) (Heffner and Masterton, 1978)
- 5- *Felis catus* - cat (Wakeford and Robinson, 1974b)
- 6- *Homo sapiens* - human (Zwislocki and Feldman, 1956)
- 7- *Homo sapiens* - human (click) (Klumpp and Eady (1956)

References:

- Don, M., and Starr, A. (1972) Lateralization performance of squirrel monkey (*Samiri sciureus*) to binaural click signals. *J. Neurophysiol.* 35, 493-500.
- Heffner, H. and Masterton, B. (1978) Contribution of auditory cortex to hearing in the monkey (*Macaca mulatta*). In D.J. Chivers and J. Herbert (eds), *Recent Advances in Primatology*, Vol I. Academic Press: New York, pp. 735-754.
- Houben, D., and Gourevitch, G. (1979) Auditory lateralization in monkeys: An examination of two cues serving directional hearing. *J. Acoust. Soc. Amer.* 66, 1057-1063.
- Klumpp, R.G., and Eady, H.R. (1956) Some measurements of interaural time difference thresholds. *J. Acoust. Soc. Amer.* 28, 859-860.
- Wakeford, O.S., and Robinson, D.E. (1974b) Lateralization of tonal stimuli by the cat. *J. Acoust. Soc. Amer.* 55, 649-652.
- Wegener, J.G. (1974) Interaural intensity and phase angle discrimination by rhesus monkeys. *J. Speech and Hear. Res.* 17, 638-655.
- Zwislocki, J., and Feldman, R.S. (1956) Just noticeable differences in dichotic phase. *J. Acoust. Soc. Amer.* 28, 860-864.

Table M101-0. Interaural time discrimination thresholds as a function of frequency.

Frequency	1	2	3	4	5	6	7
click	67			27			28
250		121				30	
500		98			32	18	
750		53					
1000		52	53		31.4	13	
1250		50				19	
1500		44					
1750		60					
2000		52			82		

Notes:

1- Operant conditioning for food using the method of constant stimuli. Animals pulled a lever on the right or left depending on which ear received the temporally leading signal. Trains of clicks (32 per sec, about 60 dB above the experimenter's threshold) delivered through earphones. Data shown for animal E for which behavior seemed most consistent. Median threshold for three other animals was 118 microsec. Functions also obtained relating the percent of responses to the right lever as a function of interaural time difference (not shown here). 85% correct. N=1.

2- Operant conditioning for food using method of constant stimuli. Animals made an observing response initiating a trial. Two tone bursts were presented binaurally through earphones, each 250 msec in duration, separated by 250 msec of silence (10 msec rise/fall times). One ear received identical tone bursts in each interval, while for the other ear, the second tone burst (the "comparison" tone) was delayed in time relative to the first ("standard tone"). Standard tone at 60 dB SPL. Means: N=3.

3- Operant conditioning for food reward using method of constant stimuli. Animals trained to press a key to the right for signals leading in time to the right ear, and to press the left key for leading signals to the left ear. Earphones held in place with a helmet. Signals were 1000 Hz tone bursts, 500 msec in duration, 3 msec rise-fall times, at 40 dB SPL, separated by 500 msec of silence. 75% correct. Means: N=9.

4- Operant conditioning for food using a method of constant stimuli. Animals trained to press a lever on the right or left, indicating the side of midline of the temporally leading signal. Clicks at least 40 dB SL. N=1.

5- Instrumental shock avoidance using the method of constant stimuli. Animals trained to exit one arm of a triple grill box and to enter one of the other two arms. Signals were 500 msec tone bursts at 70 dB SPL with 50 msec rise/fall times presented through "pinna insert" earphones held in place with a leather helmet. Animals were presented with repeating 500 msec bursts (separated by 1.17 sec of silence) with a particular interaural disparity in time. The discriminative stimulus was a reversal of the binaural disparity across the ears. Threshold defined for $P(C)=0.8$. Medians: N=3.

6- Subjects listened to pairs of one sec tone bursts (50 msec rise/fall times) of which the second was variable. The first burst always appeared in the median plane, and the interaural delay of the second was varied. Subjects reported whether the second burst appeared to the right or left of the first. Data taken as the phase difference at the 75th percentile of the right-left judgement distributions. Best interaural phase thresholds from 2.5° to 7.5°, increasing with frequency. Means: N=3.

7- Subjects listened to a pair of sounds, a standard and a variable, and judged which was further to the left as a function of the interaural delay of the variable sound. One msec clicks. Data obtained for pure tones and various noise bands not shown here. Tone data similar to those of Zwislocki and Feldman (1956). Means: N=10.

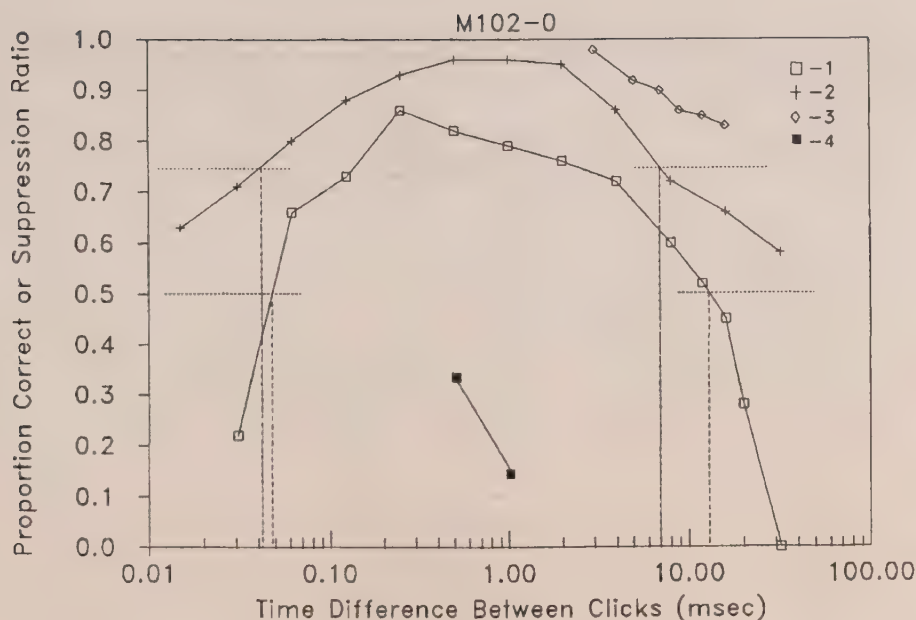


Fig. M102-0. Performance for identifying the sound source producing a temporally leading click as a function of the time interval between clicks from two sources (precedence effect).

- 1- *Rattus norvegicus* - albino rat, suppression ratio performance (Kelly, 1974)
- 2- *Rattus norvegicus* - albino rat, percent correct performance/100 (Hoeffding and Harrison, 1979)
- 3- *Felis catus* - cat, percent correct performance/100 (Cranford and Oberholtzer, 1976)
- 4- *Felis catus* - cat, percent responses/100 (Masterton and Diamond, 1964)

References:

- Cranford, J.L., and Oberholtzer, M. (1976) Role of neocortex in binaural hearing in the cat. II. The "precedence effect" in sound localization. *Brain Res.* 111, 225-139.
- Hoeffding, V., and Harrison, J.M. (1979) Auditory discrimination: Role of time and intensity in the precedence effect. *J. Exp. Anal. Behav.* 32, 157-166.
- Kelly, J.B. (1974) Localization of paired sound sources in the rat: Small time differences. *J. Acoust. Soc. Amer.* 55, 1277-1284.
- Masterton, R.B., and Diamond, I.T. (1964) Effects of auditory cortex ablation on discrimination of small binaural time differences. *J. Neurophysiol.* 27, 15-36.

Table M102-0. Performance for identifying the sound source producing a temporally leading click as a function of the time interval between clicks from two sources (precedence effect).

Inter-Click-Interval (msec)	Percent Correct or Responses/100 or Suppression Ratio			
	1	2	3	4
0.015		0.63		
0.031	0.22	0.71		
0.062	0.66	0.8		
0.125	0.73	0.88		
0.25	0.86	0.93		
0.5	0.82	0.96		0.33
1	0.79	0.96		0.14
2	0.76	0.95		
3			0.98	
4	0.72	0.86		
5			0.92	
7			0.90	
8	0.6	0.72		
9			0.86	
12	0.52		0.85	
16	0.45	0.66	0.83	
20	0.28			
32	0	0.58		

Notes:

1- Classically conditioned suppression of an ongoing water-reinforced licking response using a method of constant stimuli. Animals were presented with an ongoing train of clicks (50 msec pulses applied to tweeter loudspeakers, about 60 dB SPL (A scale), repeated 1/sec). Sources were separated by 180°, and clicks were delayed by the indicated inter-click-interval to the right channel. The conditioned stimulus was a reversal of the delay (i.e. from left-right to right-left). Medians: N=2 to 5.

These data can be interpreted based on the perceptions of human observers hearing similar sounds. At short intervals (0.04 to 3 msec), the two clicks fuse into a single sound image arising from the side with the leading click (precedence effect). Intervals less than about 40 microsec do not lead to lateralized sound images. Intervals greater than about 3 msec lead to the perception of double sound images which are not strongly lateralized. Rats behaved as if perceiving these sounds similarly.

2- Operant conditioning for liquid food using a method of constant stimuli. Two speakers produced clicks with either the left or right speaker leading the other. Animals initiated a trial and then were rewarded for pressing a left lever for left-leading clicks and the right lever for right-leading clicks. Clicks were 50 microsec impulses to loudspeakers separated by 180°, at about 87 dB SPL (peak). Medians: N=4.

3- Operant conditioning for food reward using a method of constant stimuli. Animals were trained to listen to clicks from two speakers separated by 90° azimuth, and to approach the speaker emitting the leading or earliest click. Clicks were 500 microsec electrical pulses to loudspeakers. Following unilateral auditory cortex lesions, animals made significantly more errors when the leading speaker was located opposite to the side of the lesion. Means: N=5.

4- Instrumental shock avoidance using a method of constants. Cats with large, bilateral lesions of auditory cortex wore earphones and were trained to detect a change in the interaural time delay between clicks (30 microsec electrical pulses) to the right and left earphones. Lesioned animals relearned the discrimination. Means: N=2.

M103-0

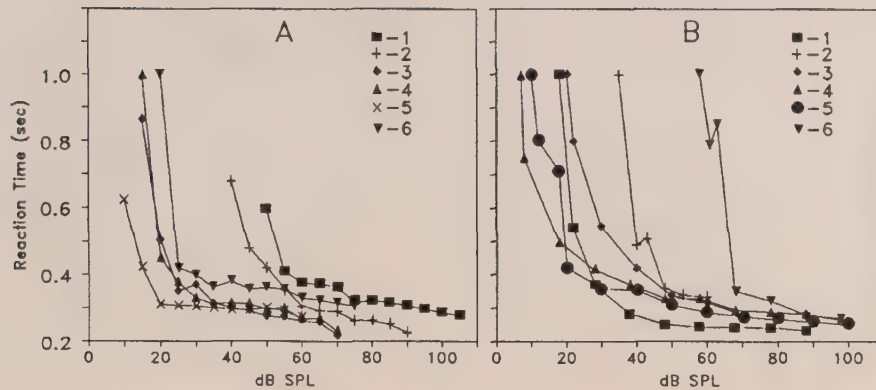


Fig. M103-0, A,B. Latency of response as a function of tone intensity in two primates.

A. *Saimiri sciureus* - squirrel monkey (Green, 1975)

- 1- 250 Hz
- 2- 500 Hz
- 3- 1000 Hz
- 4- 4000 Hz
- 5- 8000 Hz
- 6- 32000 Hz

B. *Macaca mulatta* - rhesus monkey (Pfungst, Hienz, Kimm, and Miller, 1975)

- 1- noise
- 2- 125 Hz
- 3- 250 Hz
- 4- 1000 Hz
- 5- 4000 Hz
- 6- 45000 Hz

References:

- Green, S. (1975) Auditory sensitivity and equal loudness in the squirrel monkey (*Saimiri sciureus*). J. Exp. Anal. Behav. 23, 255-264.
- Pfungst, B.E., Hienz, R., Kimm, J., and Miller, J. (1975) Reaction-time procedure for measurement of hearing. I. Suprathreshold functions. J. Acoust. Soc. Amer. 57, 421-430.

Table M103-0, A,B. Latency of response as a function of tone intensity in two primates.

(A)						(B)					
dB SPL	Reaction Time (msec)					dB SPL	Reaction Time (msec)				
1	2	3	4	5	6	1	2	3	4	5	6
10				625		7			1k		
15		865	1k	423		8			750		
20		505	450	310	1k	10				1k	
25		350	375	307	420	12				800	
30		370	330	305	400	18	1k		500	710	
35		315	310	300	360	20			1k	418	
40	680	300	315	295	380	22	540		800		
45	480	290	312	295	355	28	370		415		
50	595	420	275	295	300	30			545	358	
55	410	358	270	300	290	35		1k			
60	375	305	260	265	270	38	280		370		
65	370	290	255	270	265	40		490	418	352	
70	365	289	220	230		43		510			
75	315	262			305	48	250	360	330		
80	320	260				50			335	308	
85	315	250				53		340			
90	305	225				58	242		328	1k	
95	295					60		332	317	285	
100	285					61					790
105	275					63					850
						68	240		295		350
						70			278	275	
						78	238		290	318	
						80				265	
						88	230		280	275	
						90				257	
						98			265	267	
						100				249	

Notes:

These data (and those of Fig. M104-0) were obtained, in part, as a way to scale tone loudness for animals using response latency as a criterion.

A) Instrumental shock-avoidance using the method of constant stimuli. Animals were trained to hold down a bar (initiating a tone signal within a certain time), and then to release the bar in the presence of the tone in order to avoid shock. Signals delivered through earphones had 10 msec rise/fall times. Means: N=4.

Data were also obtained at several other frequencies, and using an operant (food reward) paradigm (not shown). The avoidance and operant paradigms produced very similar latency data.

B) Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to depress a key ("observing response") which produced a tone presentation within a variable time. Releasing the key within 1 sec of tone onset was scored as a "hit." Headphones were used. Data for animal M2.

Data were obtained at several other frequencies (not shown). Similar experiments also carried out with human observers for a comparison of the data from latency measures and direct loudness estimates.

M104-0

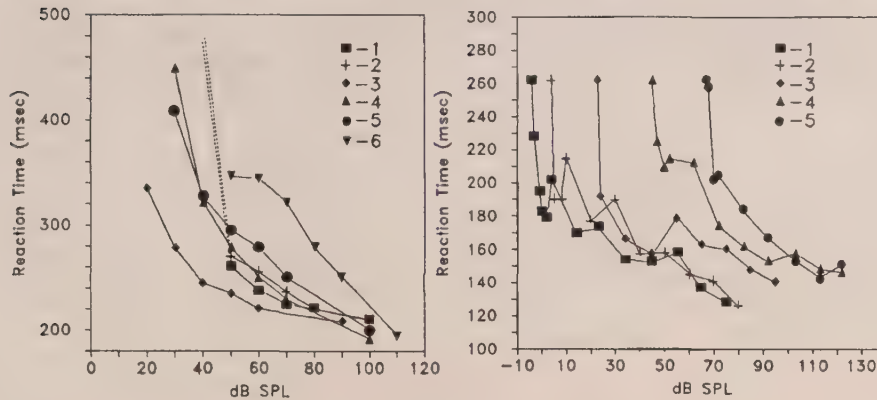


Fig. M104-0, A,B. Latency of response as a function of tone intensity in two mammals.

A. *Macaca iris* (*M. fascicularis*) - crab-eating macaque (Stebbins, 1966)

- 1- 250 Hz
- 2- 500 Hz
- 3- 1000 Hz
- 4- 5000 Hz
- 5- 10000 Hz
- 6- 15000 Hz

B. *Oryctolagus cuniculus* - New Zealand white rabbit (Martin, Lonsbury-Martin, and Kimm, 1980).

- 1- 22624 Hz
- 2- 8000 Hz
- 3- 4000 Hz
- 4- 1414 Hz
- 5- 354 Hz

References:

- Martin, G., Lonsbury-Martin, B., Kimm, J. (1980) A rabbit preparation for neuro-behavioral research. *Hear. Res.* 2, 65-78.
- Stebbins, W.C. (1966) Auditory reaction time and the derivation of equal loudness contours for the monkey. *J. Exp. Anal. Behav.* 9, 135-142.

Table M104-0, A,B. Latency of response as a function of tone intensity in two mamma

(A)							(B)					
dB SPL	Reaction Time (msec)						dB SPL	Reaction Time (msec)				
	1	2	3	4	5	6		1	2	3	4	5
20			335				-4	262				
30			278	450	408		-3	228				
40			245	322	327		-1	195				
50	260	270	235	278	295	346	0	183				
60	238	255	220	250	278	344	2	179				
70	225	237		230	250	322	4	202	262			
80	220	220				278	5		190			
90			208			250	8		190			
100	210	209		192	200		10		215			
110						194	14	170				
							20		177			
							23	173		262		
							24			192		
							30		190			
							34	154		166		
							40		157			
							45	152		157	262	
							47				225	
							50		158		210	
							52				215	
							55	158		179		
							60		145			
							62				212	
							65	137		163		
							67					262
							68					258
							70		141			202
							72				175	204
							73			160		
							80		126			
							82				162	184
							85			148		
							92				153	167
							95			140		
							103				158	153
							113				148	143
							122				146	151

Notes:

See Notes for Fig. M103-0. See Gerken and Sandlin (1977) for similar reaction time data at 250 Hz and 4 kHz for *Felis catus* (cat), and for an analysis of the effects of procedural variables on reaction time-intensity functions.

A. Operant conditioning for food reward using a method of constant stimuli. Animals were trained to make an observing response (key press) in the presence of a light, and to release the key in the presence of a tone signal. Earphones were used. Data for animal M-1. A second animal was tested (data not shown here).

B. Classical conditioning of the nictitating membrane. See Notes for Fig. M27-0.

N=1.

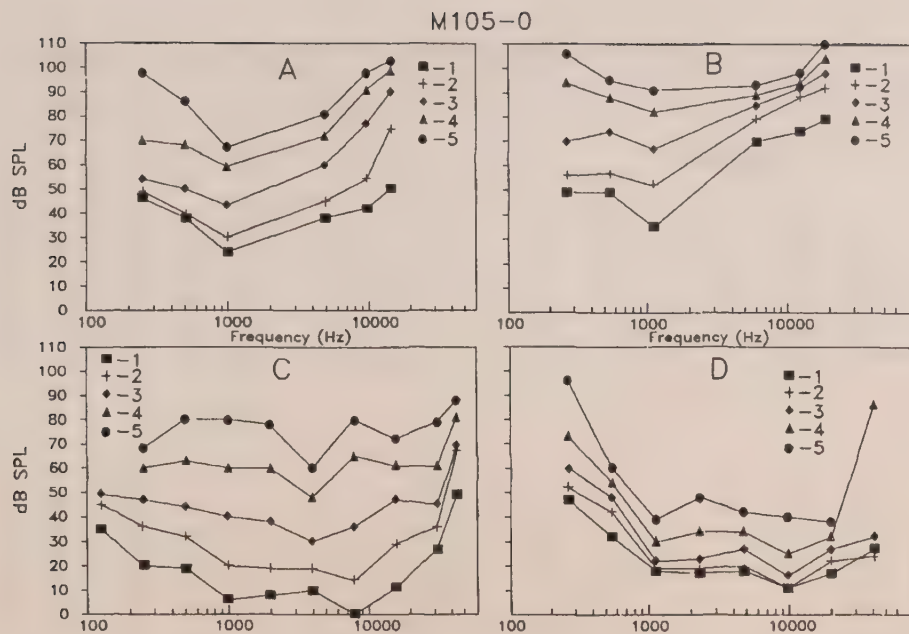


Fig. M105-0. Equal-latency contours for sound detection in several primates.

A. *Macaca iris* (*M. fascicularis*) - crab-eating macaque, animal M-1 (Stebbins, 1966)
Criterion (msec): 1- 350; 2- 300; 3- 250; 4- 225; 5- 215

B. *Macaca iris* (*M. fascicularis*) - crab-eating macaque, animal M-2 (Stebbins, 1966)
Criterion (msec): 1- 350; 2- 300; 3- 275; 4- 260; 5- 250

C. *Macaca mulatta* - rhesus monkey, animal M2 (Pfingst, Hienz, Kimm, and Miller, 1975)
Criterion (msec): 1- >1000; 2- 486; 3- 368; 4- 319; 5- 290

D. *Saimiri sciureus* - squirrel monkey, animal 5 (Green, 1975)
Criterion (msec): 1- Absolute threshold; 2- 500; 3- 400; 4- 330; 5- 300

References:

- Green, S. (1975) Auditory sensitivity and equal loudness in the squirrel monkey (*Saimiri sciureus*). *J. Exp. Anal. Behav.* 23, 255-264.
- Pfingst, B.E., Hienz, R., Kimm, J., and Miller, J. (1975) Reaction-time procedure for measurement of hearing. I. Suprathreshold functions. *J. Acoust. Soc. Amer.* 57, 421-430.
- Stebbins, W.C. (1966) Auditory reaction time and the derivation of equal loudness contours for the monkey. *J. Exp. Anal. Behav.* 9, 135-142.

Table M105-0. Equal-latency contours for sound detection in several primates.

Frequency (Hz)	dB SPL					Frequency (Hz)	dB SPL				
Table A						Table B					
	1	2	3	4	5		1	2	3	4	5
250	46	49	54	70	98	250	49	56	70	94	106
500	38	40	50	68	86	500	49	57	74	88	95
1000	24	30	43	59	67	1000	35	52	67	82	91
5000	38	45	60	72	81	5000	70	79	85	89	93
10000	42	54	77	91	98	10000	74	88	92	94	98
15000	50	75	90	99	103	15000	79	92	98	104	110

Table C						Table D					
	1	2	3	4	5		1	2	3	4	5
125	35	45	49			250	47	52	60	73	96
250	20	36	47	60	68	500	32	42	48	54	60
500	19	32	44	63	80	1000	18	19	22	30	39
1000	6	20	40	60	80	2000	17	19	23	34	48
2000	8	19	38	60	78	4000	18	20	27	34	42
4000	10	19	30	48	60	8000	11	11	16	25	40
8000	0	14	36	65	80	16000	17	22	27	32	38
16000	11	29	47	61	72	32000	27	24	32	86	
32000	27	36	45	61	79						
45000	49	67	69	81	88						

Notes:

In all above studies, the lines connect sound pressure levels producing the given criterion response latency in a tone detection task.

A. Operant conditioning for food reward using a method of constant stimuli. Animals were trained to make an observing response (key press) in the presence of a light, and to release the key in the presence of a tone signal. Earphones were used. Data for animal M-1. Based on intensity-latency data from Fig. M104-0A.

B. Same as A. Data from animal M-2.

C. Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to depress a key ("observing response") which produced a tone presentation within a variable time. Releasing the key within 1 sec of tone onset was scored as a "hit." Headphones were used. Data for animal M2 (intensity-latency data shown in Fig. M103-0B). Similar experiments also carried out with human observers for a comparison of the data from latency measures and direct loudness estimates (see Fig. M106-0).

D. Instrumental shock-avoidance using the method of constant stimuli. Animals were trained to hold down a bar (initiating a tone signal within a certain time), and then to release the bar in the presence of the tone in order to avoid shock. Signals delivered through earphones had 10 msec rise/fall times. Animal #5, based on data from Fig. M103-0A. Data were also obtained using an operant (food reward) paradigm (not shown). The avoidance and operant paradigms produced very similar latency data and equal-latency contours.

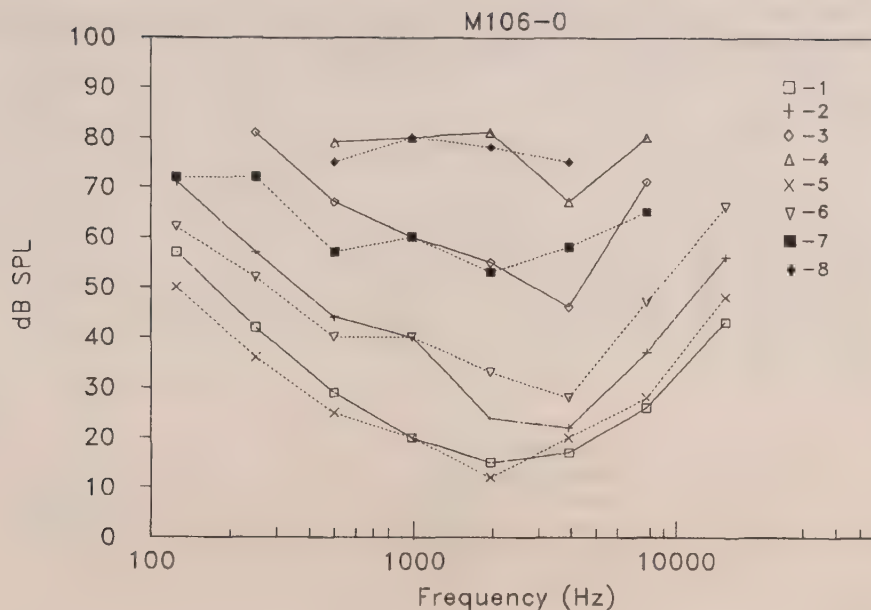


Fig. M106-0. Contours defined by equal response latency and equal loudness judgments in *Homo sapiens* (human) (Pfingst, Hienz, Kimm, and Miller, 1975).

- 1- Latency criterion (msec): 233
- 2- Latency criterion (msec): 190
- 3- Latency criterion (msec): 170
- 4- Latency criterion (msec): 155
- 5- Level of 1000 Hz reference tone: 20 dB
- 6- Level of 1000 Hz reference tone: 40 dB
- 7- Level of 1000 Hz reference tone: 60 dB
- 8- Level of 1000 Hz reference tone: 80 dB

Solid lines: equal-latency
Dashed lines: equal loudness

Reference:

Pfingst, B.E., Hienz, R., Kimm, J., and Miller, J. (1975) Reaction-time procedure for measurement of hearing. I. Suprathreshold functions. *J. Acoust. Soc. Amer.* 57, 421-430.

Table M106-0. Contours defined by equal response latency and equal loudness judgments in *Homo sapiens* (human) (Pfungst, Hienz, Kimm, and Miller, 1975).

Frequency (Hz)	dB SPL							
	1	2	3	4	5	6	7	8
125	57	71			50	62	72	
250	42	57	81		36	52	72	
500	29	44	67	79	25	40	57	75
1000	20	40	60	80	20	40	60	80
2000	15	24	55	81	12	33	53	78
4000	17	22	46	67	20	28	58	75
8000	26	37	71	80	28	47	65	
16000	43	56			48	66		

Notes:

Equal-latency experiments (solid lines).

Human subjects were tested using a paradigm very similar to the one used in experiments on monkeys as described in Fig. M103-0 for the monkey. Subjects wearing earphones were instructed to depress a key in the presence of a signal light, and then to release the key as quickly as possible following tone onset. Reaction time functions of signal level were used to construct the above family of equal-latency functions. These are the interpolated SPLs corresponding to the given response latencies. One subject (H1).

Equal-loudness experiments (dashed lines).

Human subjects were presented with a reference stimulus (a one sec, 1000 Hz tone), and a tone of different frequency, also for one sec. The subjects indicated which of these two tones were louder. The 1000 Hz reference was varied in 4 dB steps, and the comparison tones were varied in 10 dB steps. For each intensity of the comparison tone, the percentage of times the reference was judged to be louder was plotted as a function of the reference tone level. Equal-loudness contours were then derived from the 50% points on these functions. One subject (H1).

These data illustrate the relation between equal loudness estimated derived from direct loudness judgements, and from response latency.

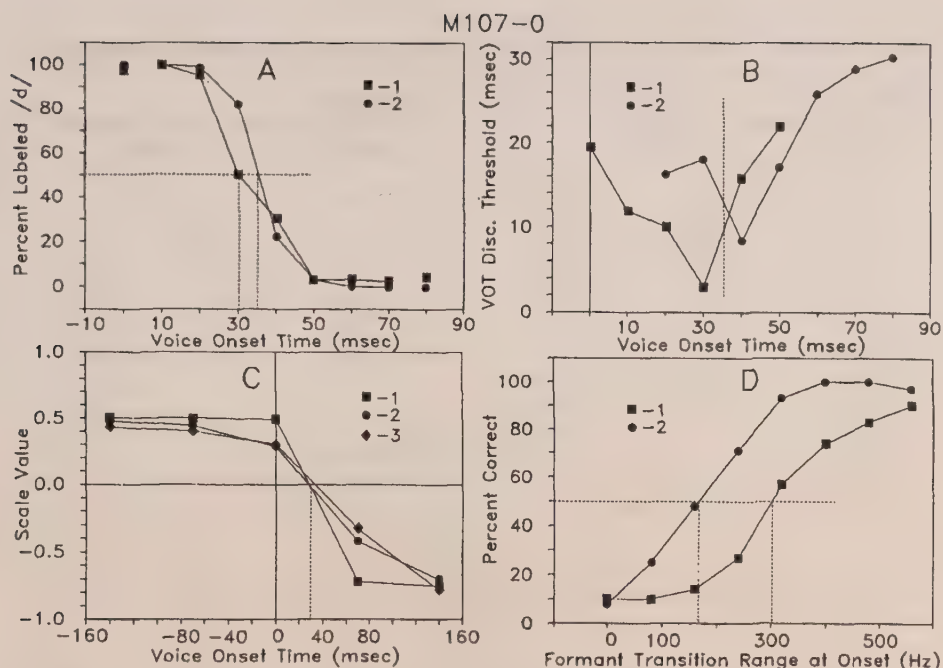


Fig. M107-0. Aspects of human speech discrimination by several mammals.

A. Labeling of /ta/ and /da/ speech sounds as a function of voice onset time in chinchilla and English-speaking humans (Kuhl and Miller, 1975).

1- *Chinchilla laniger* - chinchilla. 2- *Homo sapiens* - human

B. Voice onset time discrimination thresholds as a function of voice onset time in *Chinchilla laniger* - chinchilla (Kuhl, 1981)

1- Discrimination of change from lower to higher VOT values

2- Discrimination of change from higher to lower VOT values

C. Labeling of /ba/ and /pa/ as a function of voice onset time by *Macaca mulatta*. (rhesus monkey) (Waters and Wilson, 1976).

1- Animal 1. 2- Animal 5. 3- Animal 7.

D. Discrimination of formant transitions (in Hz) along the /ba/ - /da/ continuum in humans and monkeys (Sinnott, Beecher, Moody, and Stebbins, 1976).

1- *Macaca nemestrina*, *Cercopithecus aethiops*, *Macaca fascicularis* (Old World monkeys). 2- *Homo sapiens* - human

References:

- Kuhl, P.K. (1981) Discrimination of speech by nonhuman animals: Basic auditory sensitivities conducive to the perception of speech-sound categories. *J. Acoust. Soc. Amer.* 70, 340-349.
- Kuhl, P.K. and Miller, J.D. (1975) Speech perception by the chinchilla: Voiced-voiceless distinction in alveolar plosive consonants. *Science*, 190, 69-72.
- Sinnott, J.M., Beecher, M.D., Moody, D.B., and Stebbins, W.C. (1976) Speech sound discrimination by monkeys and humans. *J. Acoust. Soc. Amer.* 60, 687-695.
- Waters, R.S., and Wilson, W.A. (1976) Speech perception by rhesus monkeys: The voicing distinction in synthesized labial and velar stop consonants. *Percept. Psychophys.* 19, 285-289.

Table M107-0. Aspects of human speech discrimination by several mammals.

TABLE A

Voice Onset Time (msec)	Percent /d/	
	1	2
0	97	100
10	100	100
20	95	99
30	50	82
40	30	22
50	3	3
60	3	0
70	2	0
80	4	0

TABLE B

Voice Onset Time (msec)	VOT Threshold (msec)	
	1	2
0	19.5	
10	11.9	
20	10	16.3
30	3	18.1
40	15.8	8.4
50	21.9	17.1
60		25.8
70		28.8
80		30.3

TABLE C

Voice Onset Time (msec)	Scale Value		
	1	2	3
-140	0.5	0.48	0.43
-70	0.5	0.44	0.4
0	0.49	0.28	0.3
70	-0.72	-0.42	-0.33
140	-0.75	-0.7	-0.78

TABLE D

Formant Transition (Hz)	Percent Correct	
	1	2
0	10	8
80	10	25
160	14	48
240	27	71
320	57	93
400	74	100
480	83	100
560	90	97

Notes:

A. Voice onset time (VOT) is the time between the onset of the plosive burst of certain consonants and the time at which voicing of the vowel begins. Some syllable pairs (e.g. /da/-/ta/) are discriminated on the basis of the VOT. See also Kuhl and Miller (1978) for more chinchilla data on identification of synthetic VOT stimuli.

Instrumental shock avoidance using a method of constant stimuli. Animals were trained to cross a barrier following one synthetic speech sound (e.g. a VOT of 0 msec, perceived as /da/ by humans), and not to cross for another sound with a VOT of 80 msec, perceived as /ta/). Tested in generalization to other signals of different VOT. The "phonetic boundary" = 33.5 msec for chinchilla; 35.2 msec for humans. Means: N=2.

B. Same methods as (A), using a staircase method. Animals trained on a "same-different" task. "Same" trial - seven presentations of the same syllable. "Different" trial - last 3 syllables different from 1st 4. The lowest VOT thresholds occur when the change crosses the phonetic boundary as defined in (A). Results from (A) and (B) help establish categorical perception for human speech in chinchillas. Means: N=3.

C. Instrumental shock avoidance ("go, no-go" barrier crossing) using the method of constant stimuli. Negative VOTs indicate "prevoicing." Animals first trained on extreme VOT values and then tested at intermediate values. The "scale" values were derived so that 0 indicates the VOT that lies between two categories. Means: N=4.

D. Operant conditioning for food using constant stimuli. Observing response initiated a repeating background of a given syllable. Releasing the response after the a single different syllable was rewarded. Synthesized syllables differed in the direction and amount of 1st and 2nd formant frequency change during first 50 msec (sounds like /ba/ for upward change; /da/ for downward change). Two animals discriminated differences from /ba/, and others from /da/. Means: N=4.

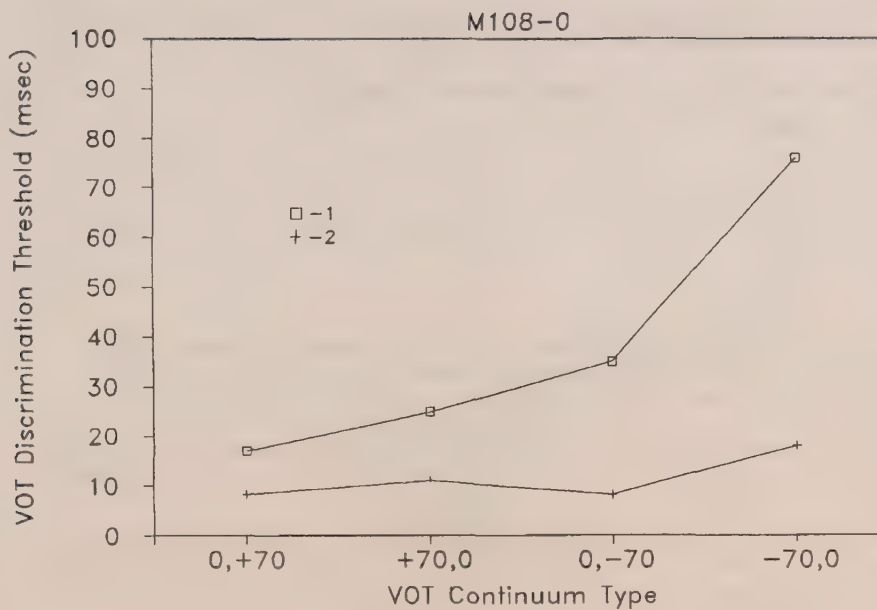


Fig. M108-0. Voice onset time discrimination along four continua in Old World monkeys and humans (Sinnott and Adams, 1987)

- 1- *Macaca fuscata* - Japanese macaque
Cercopithecus aethiops - vervet monkey
- 2- *Homo sapiens* - human

Reference:

Sinnott, J.M., and Adams, F.S. (1987) Differences in human and monkey sensitivity to acoustic cues underlying voicing contrasts. *J. Acoust. Soc. Amer.* 82, 1539-1547.

Table M108-0. Voice onset time discrimination along four continua in Old World monkeys and humans (Sinnott and Adams, 1987)

VOT Continuum Type	VOT Discrimination Threshold (msec)	
	1	2
0,+70	17	8.3
+70,0	25	11
0,-70	35	8.2
-70,0	76	18

Notes:

Operant conditioning for a food reward using a method of constant stimuli. Animals were trained to make an observing response which initiated a series of identical "repeating standard" synthetic syllables. At a variable time following the initiation of the trial, a different syllable was substituted for the standard. A response within two sec was rewarded. The plosive burst was a noise burst, and the vowel sound was a multi-formant complex. The voice onset time (VOT) is the time from burst onset to voicing onset.

The condition 0,+70 refers to the case in which a 0 msec VOT (/ba/) was the standard, and the VOT of the "target" syllable varied toward longer VOTs (i.e. toward /pa/). The threshold for this case and the reverse (0,-70) estimate the acuity in detecting nonsimultaneous onsets of the burst and the voicing.

The condition +70,0 refers to the case in which the standard is a /pa/ and the target varied toward shorter VOTs (/ba/). The threshold in this case is an estimate of acuity for discriminating a change in the duration of the aspiration noise.

The condition -70,0 refers to the case in which the standard is a "prevoiced" /ba/ and the VOT of the target varied toward a normal /ba/. The threshold here is an estimate of the ability to discriminate changes in voicing duration.

Means: N=4 monkeys, N=3 humans.

This paper also reported that the VOT discrimination threshold remained relatively constant as a function of overall sensation level for humans, and declined slightly toward higher sensation levels for the monkeys.

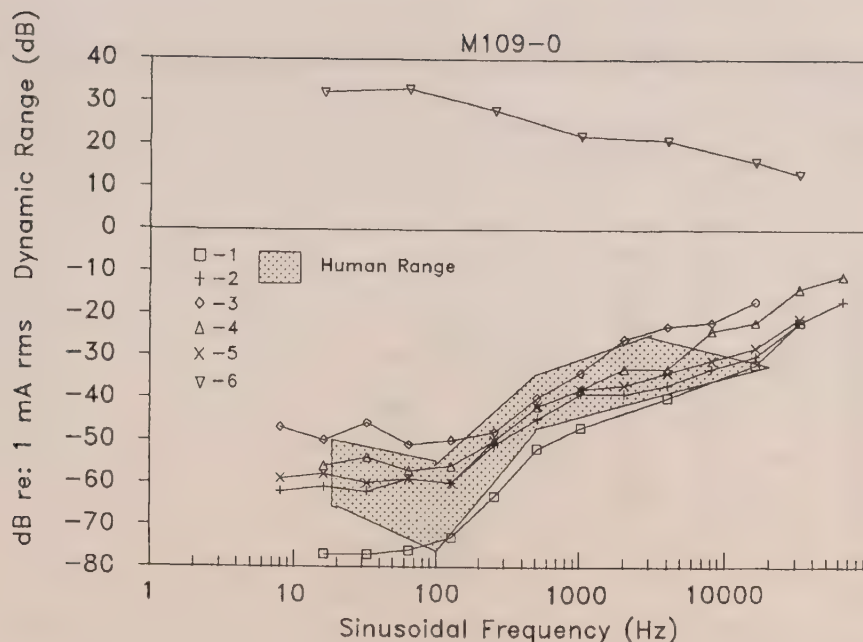


Fig. M109-0. Thresholds for the detection of electrical stimulation of the cochlea in macaque monkeys.

- 1- *Macaca mulatta* or *Macaca nemistrina* - rhesus or pig-tailed macaque, subject PU-R
- 2- *Macaca mulatta* or *Macaca nemistrina* - subject RI-L-1
- 3- *Macaca mulatta* or *Macaca nemistrina* - subject GR-L-1
(Pfungst, Donaldson, Miller, and Spelman, 1979)
- 4- *Macaca mulatta* - rhesus monkey, subject MA-R-1 (Pfungst, Burnett, and Sutton, 1979)
- 5- *Macaca* sp. - macaque monkey, (Pfungst, Spelman, and Sutton, 1980)
- 6- Dynamic range for #4 above.

Shaded area shows the range of threshold values for *Homo sapiens* (human), as reviewed by Pfingst, Glass, Spelman, and Sutton (1985).

References:

- Pfungst, B.E., Burnett, P.A., and Sutton, D. (1983) Intensity discrimination with cochlear implants. *J. Acoust. Soc. Amer.* 73, 1283-1292.
- Pfungst, B.E., Donaldson, J.A., Miller, J.M., and Spelman, F.A. (1979) Psychophysical evaluation of cochlear prostheses in a monkey model. *Ann. Otol. Rhinol. Otolaryngol.* 88, 613-.
- Pfungst, B.E., Glass, I., Spelman, F.A., and Sutton, D. (1985) Psychophysical studies of cochlear implants in monkeys: Clinical implications. In R.A. Schindler and M.M. Merzenich (eds), *Cochlear Implants*. Raven Press: New York, pp 305-321.
- Pfungst, B.E., Spelman, F.A., and Sutton, D. (1980) Operating ranges for cochlear implants. *Ann. Otol. Rhinol. Laryngol.* 89, (suppl. 66), 1-4.

Table M109-0. Thresholds for the detection of electrical stimulation of the cochlea in macaque monkeys.

Frequency (Hz)	dB re: 1 milliamp (rms) or dynamic range in dB				
	1	2	3	4	5
8		-62	-47		-59
16	-77	-61	-50	-56	-58
32	-77	-62	-46	-54	-60
63	-76	-59	-51	-57	-59
125	-73	-60	-50	-56	-60
250	-63	-51	-48	-50	-50
500	-52	-45	-40	-42	-42
1000	-47	-39	-34	-38	-38
2000		-39	-26	-33	-37
4000	-40	-37	-23	-33	-34
8000		-33	-22	-24	-31
16000	-32	-30	-17	-22	-28
32000	-22	-22		-14	-21
64000		-17		-11	

Notes:

1-3- Operant conditioning for a food reward using a method of constant stimuli. Animals were trained to press a key following a light signal, and to release the key upon presentation of electrical stimulation of scala tympani intra-cochlear electrodes. N=1 for each function plotted. Each function is for a different animal, and a different position of the stimulating electrode pair.

4- Same procedures as #1. Electrode separation: 3.4 mm.

5- Same procedures as #1. This study also obtained thresholds for balanced biphasic pulses of periods ranging from 0.1 to 100 msec, and repetition rates ranging from 10 to 10000 Hz. There is a small effect of pulse repetition rate on threshold (higher rates have lower thresholds), and a large effect of pulse duration. The sensitivity and frequency response function for sinusoidal stimulation can be largely accounted for by the effective reduction in the duration of individual stimulating cycles of the sinusoid as the frequency increases. N=1.

6- For the animal tested in #4, response latency measurements were used to determine dynamic range. The electrical stimulation current levels producing latencies equal to the latencies produced by acoustic stimulation with 100 dB SPL white noise defined the upper limit of the dynamic range (maximum loudness). The points plotted here are the difference between thresholds for detection (plotted in #4) and the maximum loudness thresholds. Clearly, the dynamic range for perceptions arising from electrical stimulation are small, and declines with frequency.

The fact that the macaque thresholds correspond so closely with human thresholds helps establish the usefulness of these animal models for the development and testing of cochlear implant prostheses.

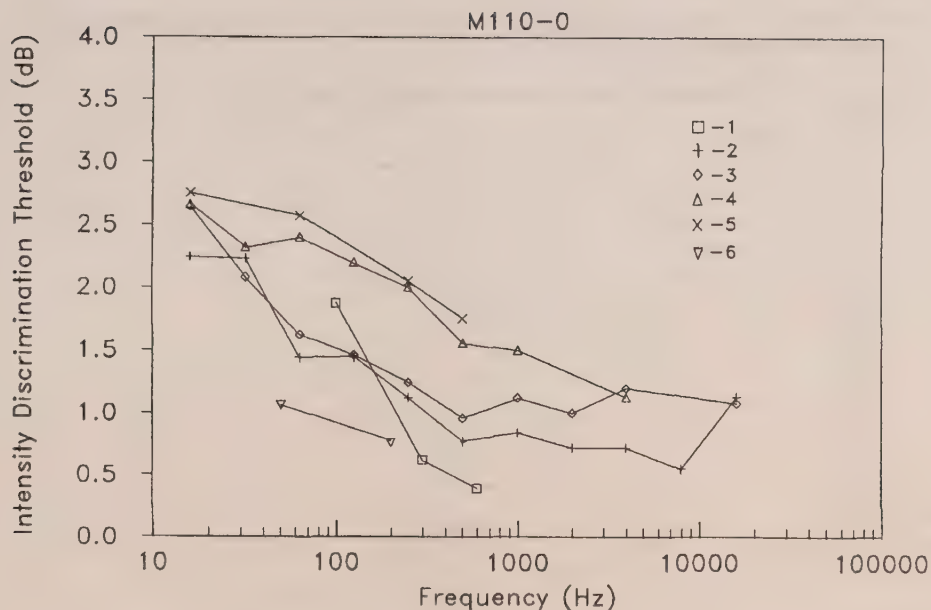


Fig. M110-0. Intensity discrimination for intracochlear electrical stimulation as a function of stimulus frequency.

1- *Macaca mulatta* - rhesus monkey (Pfungst and Rush, 1987)

2- Animal MA-R-1

3- Animal GA-L-1

4- Animal BE-R-1

5- Animal MA-L-1

Macaca mulatta - rhesus monkey (Pfungst, Burnett, and Sutton, 1987)

6- *Felis catus* - cat (Black, Steel, and Clark, 1983)

References:

- Black, R.C., Steel, A.C., and Clark, G.M. (1983) Amplitude and pulse rate difference limens for electrical stimulation of the cochlea following graded degeneration of the auditory nerve. *Acta Otolaryngol.* 95, 27-33.
- Pfungst, B.E., Burnett, P.A., and Sutton, D. (1983) Intensity discrimination with cochlear implants. *J. Acoust. Soc. Amer.* 73, 1283-1292.
- Pfungst, B.E., and Rush, N.L. (1987) Discrimination of simultaneous frequency and level changes in electrical stimuli. *Ann. Otol. Rhinol. Laryngol.* 96 (Suppl. 128), 34-37.

Table M110-0. Intensity discrimination for intracochlear electrical stimulation as a function of stimulus frequency.

Frequency (Hz)	Intensity Discrimination Threshold (dB)					
	1	2	3	4	5	6
16		2.24	2.64	2.66	2.75	
32		2.23	2.08	2.32		
50						1.06
63		1.44	1.62	2.4	2.57	
100	1.87					
125		1.44	1.46	2.2		
200						0.76
250		1.12	1.24	2	2.05	
300	0.62					
500		0.77	0.96	1.56	1.75	
600	0.39					
1000		0.84	1.12	1.5		
2000		0.72	1			
4000		0.72	1.2	1.13		
8000		0.55				
16000		1.13	1.08			

Notes:

1- Operant conditioning for a food reward using a method of constant stimuli. Animals were trained to press a key following a light signal. This produced a repeating "background" stimulus (200 msec on and 100 msec off) at a particular intensity of electrical stimulation. A release of the key when stimulus intensity changed was reinforced. Scala tympani intra-cochlear electrodes. Sinusoidal electrical signal 7 to 9 dB above detection threshold. N=1.

2-5- Same methods as #1. For each of the ears tested, stimulus intensity was adjusted to be in the center of the dynamic range for the given subject and condition. The authors note that these thresholds are about half the size of those determined in the macaque using acoustic stimulation.

2- MA-R-1. Multichannel, intracochlear implant in scala tympani

3- GA-L-1. Same as #2 but perforated basilar membrane.

4- BE-R-1. Multichannel, intracochlear implant in scala tympani

5- MA-L-1. Extra cochlear electrode array

6- Classically conditioned suppression of an ongoing response using a descending method of limits. Signals were 500 msec trains of 0.1 msec per phase biphasic pulses repeated at the indicated frequencies (rates). The conditioned stimulus was a change from a repeating background of constant pulse intensity to an alternation of intensity between successive trains. Scala tympani electrodes about 5 mm from the round window. Means: N=4.

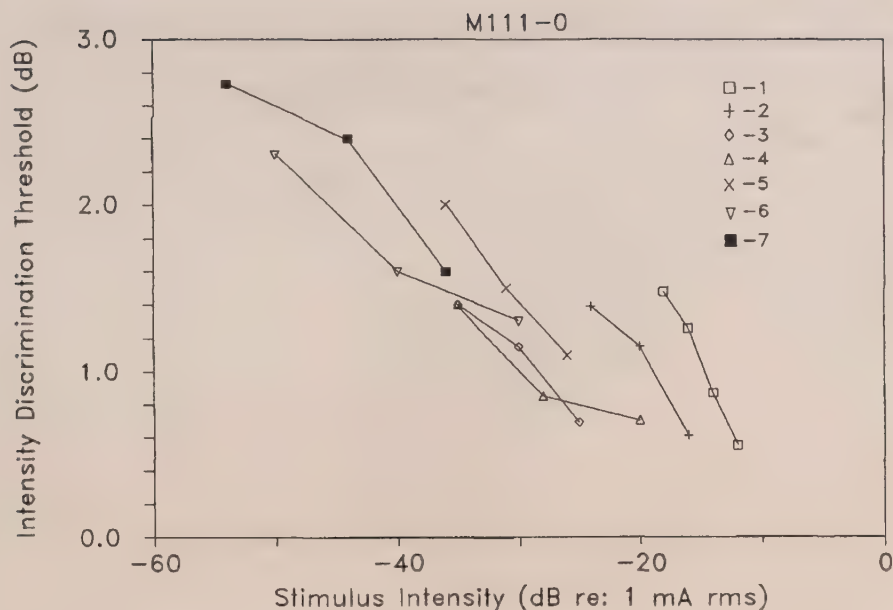


Fig. M111-0. Intensity discrimination thresholds for electrical stimulation of the cochlea in macaque monkeys as a function of stimulus intensity.

- 1- Animal GA-R-1, modiolar implant, 1.1 mm electrode spacing
- 2- Animal GA-L-1, intracochlear implant, 0.5 mm electrode spacing
- 3- Animal GA-L-1, intracochlear implant, 3.2 mm electrode spacing
- Macaca mulatta* - rhesus monkey, 1000 Hz (Pfungst, Burnett, and Sutton, 1983)
- 4- Animal C, 1000 Hz
- 5- Animal B, 1000 Hz
- 6- Animal C, 63 Hz
- 7- Animal B, 63 Hz
- Macaca mulatta* - rhesus monkey (Pfungst and Sutton, 1983)

References:

- Pfungst, B.E., Burnett, P.A., and Sutton, D. (1983) Intensity discrimination with cochlear implants. *J. Acoust. Soc. Amer.* 73, 1283-1292.
- Pfungst, B.E., and Sutton, D. (1988) Relation of cochlear implant function to histopathology in monkeys. *Ann. N.Y. Acad. Sci.* 405, 224-239.

Table M111-0. Intensity discrimination thresholds for electrical stimulation of the cochlea in macaque monkeys as a function of stimulus intensity.

Stimulus Intensity (dB re: 1 mA rms)	Intensity Discrimination Threshold (dB)						
	1	2	3	4	5	6	7
-12	0.55						
-14	0.87						
-16	1.26	0.61					
-18	1.48						
-20		1.15		0.7			
-24		1.39					
-25			0.69				
-26					1.1		
-28				0.85			
-30			1.15			1.3	
-31					1.5		
-35			1.4	1.4			
-36					2		1.6
-40						1.6	
-44							2.4
-50						2.3	
-54							2.73

Notes:

1-3- Operant conditioning for a food reward using a method of constant stimuli. Animals were trained to press a key following a light signal. This produced a repeating "background" stimulus (200 msec on and 100 msec off) at a particular intensity of electrical stimulation. A release of the key when stimulus intensity changed was reinforced. Sinusoidal electrical signals all presented within 25% and 75% of the dynamic range.

4-7- Essentially the same methods as in #1-3.

These data illustrate that the intensity discrimination threshold declines significantly toward higher stimulus intensities regardless of stimulation frequency or electrode type or location. Electrical stimulation of the human ear shows the same effects and very similar thresholds (reviewed by Pfingst, 1988).

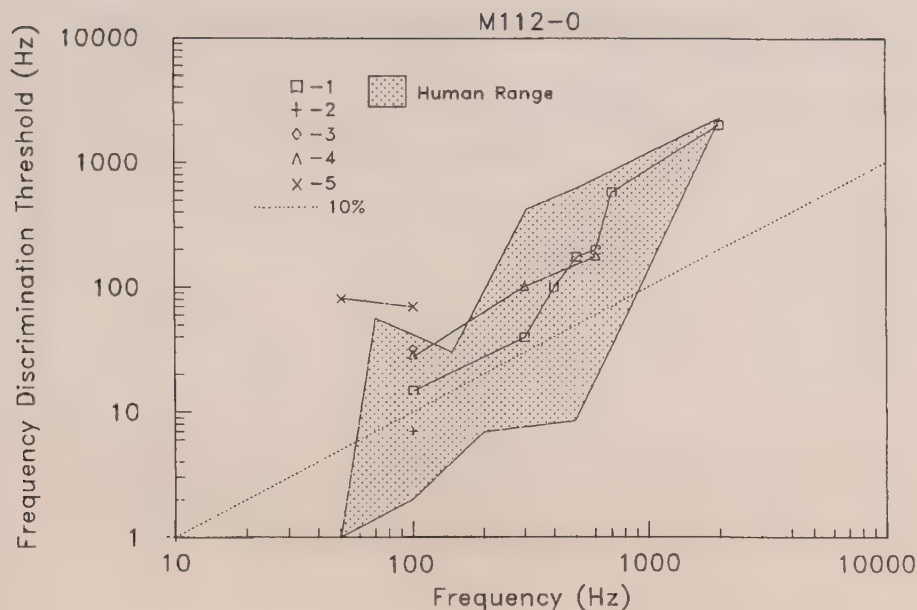


Fig. M112-0. Frequency discrimination thresholds for intracochlear electrical stimulation in primates.

- 1- *Macaca* sp. - macaque monkey, 10 dB SL (Pfungst, Evans, and Garrido, 1984)
- 2- Same as #1, 17 dB SL
- 3- Same as #1, 7 dB SL
- 4- *Macaca mulatta* - rhesus monkey (Pfungst and Rush, 1987)
- 5- *Felis catus* - cat (Black, Steel, and Clark, 1983)

The shaded area encloses the range of frequency discrimination thresholds for *Homo sapiens* (human) as reviewed by Pfingst, 1988.

References:

- Black, R.C., Steel, A.C., and Clark, G.M. (1983) Amplitude and pulse rate difference limens for electrical stimulation of the cochlea following graded degeneration of the auditory nerve. *Acta Otolaryngol.* 95, 27-33.
- Pfungst, B.E. (1988) Comparison of psychophysical and neurophysiological studies of cochlear implants. *Hear. Res.*, in press.
- Pfungst, B.E., Evans, M., and Garrido, Y. (1984) Electrical frequency discrimination: Initial results from studies in macaques. Abstracts of the 1984 West Coast Cochlear Prosthesis Workshop, 18. Cited in Pfingst, B.E. (1988) Comparison of psychophysical and neurophysiological studies of cochlear implants. *Hear. Res.*, in press.
- Pfungst, B.E., and Rush, N.L. (1987) Discrimination of simultaneous frequency and level changes in electrical stimuli. *Ann. Otol. Rhinol. Laryngol.* 96 (Suppl. 128), 34-37.

Table M112-0. Frequency discrimination thresholds for intracochlear electrical stimulation in primates.

Frequency (Hz)	Frequency Discrimination Threshold				
	1	2	3	4	5
50					81
100	15	7	32	29	70
300	40			102	
400	100				
500	175				
600	200			179	
700	580				
2000	2000				

Notes:

1-3- Operant conditioning for a food reward using a method of constant stimuli. Animals were trained to press a key following a light signal. This produced a repeating "background" stimulus (200 msec on and 100 msec off) at a particular frequency of electrical stimulation. A release of the key when stimulus frequency changed was reinforced. Scala tympani intra-cochlear electrodes.

1- 10 dB sensation level

2- 17 dB sensation level

3- 7 dB sensation level

4- Same methods as #1-3. In this experiment, each frequency difference value was presented in conjunction with a wide range of stimulus intensity differences. The percent correct functions of intensity difference were "V" shaped. The minimum percent correct value for each function was assumed to be performance which was least affected by possible loudness difference cues. Sensation level from 7 to 9 dB. N=1. The authors point out that this laborious procedure likely eliminates loudness difference cues in a frequency discrimination task, and that much of the human data in the literature (not using this control procedure) (shaded area) are likely contaminated by loudness cues to unknown extents.

5- Classically conditioned suppression of an ongoing response using a descending method of limits. Signals were 500 msec trains of 0.1 msec per phase biphasic pulses repeated at the indicated frequencies (rates). The conditioned stimulus was a change from a repeating background of constant pulse frequency to an alternation of frequency between successive trains. Scala tympani electrodes about 5 mm from the round window. Means: N=4.

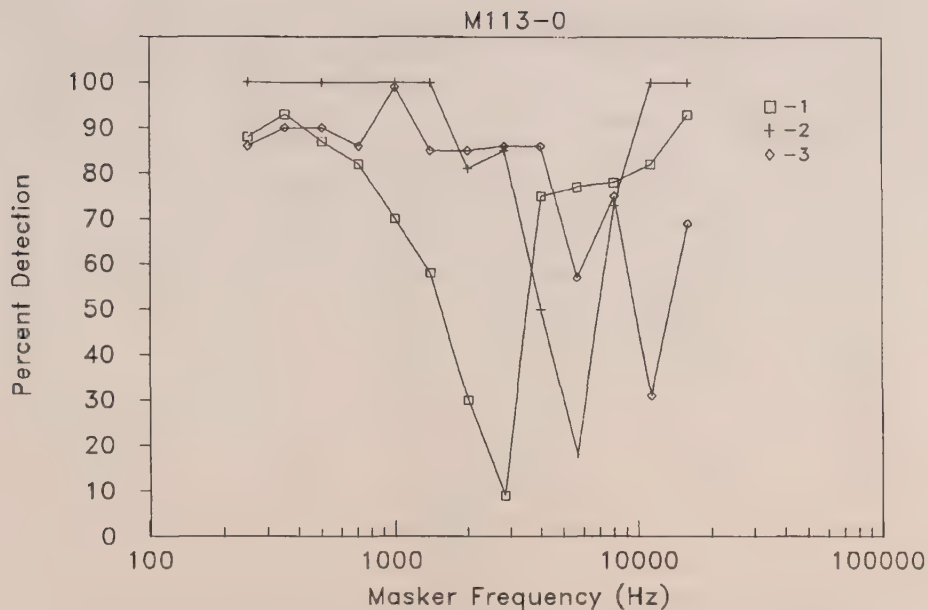


Fig. M113-0. The effect of pure tone acoustic maskers on the detection of electrical stimulation in the cochlear nucleus in *Felis catus* (cat) (Frederickson and Gerken, 1977).

- 1- Animal 188
- 2- Animal 216
- 3- Animal 220

Reference:

Frederickson, C.J., and Gerken, G.M. (1977) Masking of electrical by acoustic stimuli: Behavioral evidence for tonotopic organization. *Science* 198, 1276-1278.

Table M113-0. The effect of pure tone acoustic maskers on the detection of electrical stimulation in the cochlear nucleus in *Felis catus* (cat) (Frederickson and Gerken, 1977).

Masker Frequency (Hz)	Percent Detection		
	1	2	3
250	88	100	86
353	93		90
500	87	100	90
707	82		86
1000	70	100	99
1400	58	100	85
2000	30	81	85
2830	9	85	86
4000	75	50	86
5660	77	18	57
8000	78	73	75
11300	82	100	31
16000	93	100	69

Notes:

Operant conditioning for a food reward using the method of constant stimuli. Animals were trained to initiate trials by placing a paw in a slot. Withdrawing the paw within 1.5 sec of electrical stimulation of the cochlear nucleus (1 dB above detection threshold) resulted in reward. Maskers were 20 msec duration tone bursts at 50 dB SPL, with 3 msec rise/fall times.

Each of the three animals tested was implanted with a cochlear nucleus stimulating electrode in a slightly different location within the anteroventral area of the nucleus. The frequency specificity of the masking indicates that acoustic and electrical activation of the brain interacts, that the electrodes likely stimulated only a limited area of tonotopically organized neural tissue, and that tonotopy has implications for auditory perception as well as auditory neuroanatomy and neurophysiology.

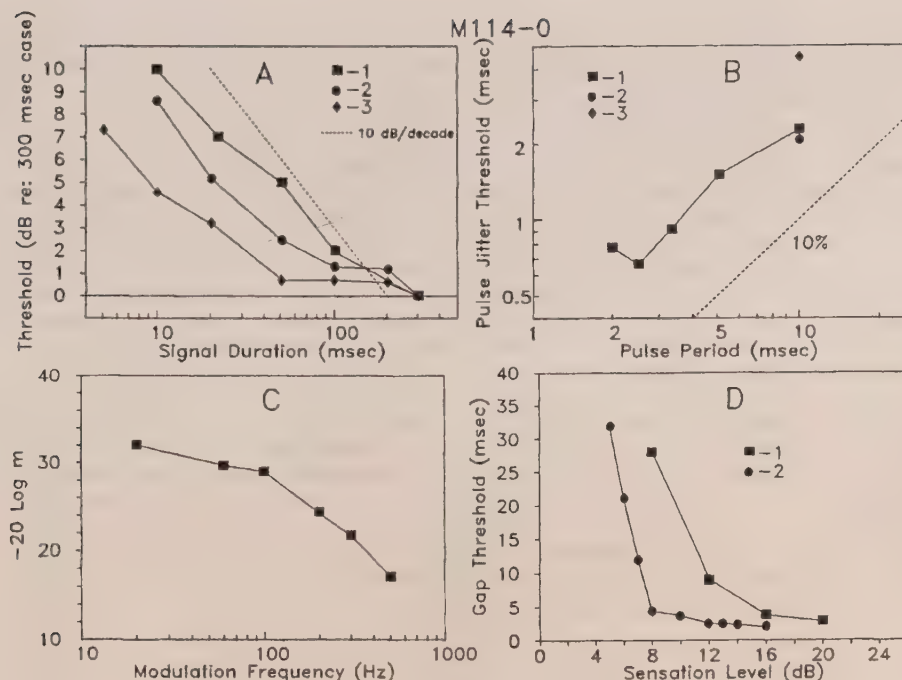


Fig. M114-0. Aspects of temporal processing of electrical stimulation of the cochlea in *Homo sapiens* (human).

A. Temporal summation at threshold (Shannon, 1983)

1- Subject LY

2- Subject CE

3- Subject CB

Dashed line indicates 10 dB per decade of duration

B. Temporal jitter detection (Shannon, 1986)

1- Comfortable loudness level

2- Minimal loudness; near threshold

3- "Loud"

Dashed line indicates a 10% period discrimination threshold

C. Amplitude modulation detection thresholds (TMTF) (Shannon, 1986)

D. Gap detection thresholds (Shannon, 1986)

1- Subject CL

2- Subject EHT

References:

Shannon, R.V. (1983) Multichannel electrical stimulation of the auditory nerve in man.

I. Basic psychophysics. *Hear. Res.* 11, 157-189.

Shannon, R.V. (1986) Temporal processing in cochlear implants. In M.J. Collins, T.J.

Glatke, and L.A. Harker (eds), *Sensorineural Hearing Loss: Mechanisms, Diagnosis, and Treatment*. University of Iowa Press: Iowa City.

Table M114-0. Aspects of temporal processing of electrical stimulation of the cochlea in *Homo sapiens* (human).

TABLE A

Signal Duration (msec)	Threshold (dB relative)		
	1	2	3
5			7.3
10	10	8.6	4.6
20		5.2	3.2
22	7		
50	5	2.5	0.7
100	2	1.3	0.7
200		1.2	0.6
300	0	0	0

TABLE B

Pulse Period (msec)	Jitter Threshold (msec)		
	1	2	3
2	0.77		
2.5	0.66		
3.33	0.92		
5	1.51		
10	2.3	2.1	4.5

TABLE D

Sensation Level (dB)	Gap Threshold (msec)	
	1	2
5		32
6		21
7		12
8	28	4.4
10		3.7
12	9	2.5
13		2.4
14		2.3
16	3.8	2
20	2.8	

TABLE C

Modulation Frequency (Hz)	-20 Log m
20	32
60	29.7
100	29
200	24.3
300	21.7
500	17.1

Notes:

A. Bekesy tracking method. 1000 Hz sinusoidal electrical signals.

1- Differential stimulation of two intracochlear electrodes.

2- Monopolar stimulation

3- Differential stimulation of two intracochlear electrodes.

B. Subjects were instructed to discriminate between two electrical pulse trains; one perfectly periodic, and the other in which the inter-pulse-interval was randomly varying (jittering) within a dome-shaped probability density function (one-half cycle of a sinusoid). Thresholds expressed in terms of the range of jitter just detectable. Pulses were biphasic with a duration a small fraction of repetition period. Compare these thresholds for a similar acoustic experiment on the goldfish (Fig. F47-0A, #4).

1- Comfortable loudness level

2- Minimal loudness; near threshold

3- "Loud"

C. Amplitude modulation detection. A 200 Hz carrier was modulated at the indicated rates, and thresholds were determined for the minimum detectable modulation depth. The value m is the modulation index which varies between 0 (no modulation) and 1.0 (100% modulation). The value -20 Log m is the modulation expressed in dB. The time constant was determined to be between 1 and 2 msec.

D. Gap detection. Subjects detected brief silent intervals within ongoing sinusoidal stimulation. All subjects achieved a gap threshold in the vicinity of 1 msec at high loudness levels.

1- 500 Hz sinusoid carrier

2- 1000 Hz sinusoid carrier

Comparisons among Vertebrates on Selected Hearing Capacities

This brief section of 13 figures brings together some of the hearing functions from the sections on the lateral line, fishes, birds, amphibians & reptiles, and mammals. The purpose here is to make several rather general points about hearing in vertebrates, and to illustrate some of the comparisons which can be made using the data presented in this book.

All figures of this section were derived from figures presented earlier using a graphics editor, Freelance Plus. Each figure of this book is stored electronically in graphical form (Freelance .DRW files), and is available on disk for a nominal charge (contact the publisher).

The origin of each function plotted is given in the figure captions.

AUDIOGRAMS

Fig. C1-0 presents the audiograms for all vertebrate species for which reasonably valid data exist, plotted together by animal group. The purpose of this figure is to give a sort of snap-shot of the amount of published data available, the number of species studied within each group, and the within-group variability in hearing range and sensitivity. Group "audiograms" were determined graphically so that generalizations could be made about the bandwidth, best frequency range, and sensitivity for each group.

Fig. C2-0 compares the audiograms for seven mammal species that are often used in auditory research and which have relatively good low frequency hearing.

Many other audiogram comparisons are possible to make using the data presented throughout the book, including all primates, rodents, carnivores, predators, prey, diurnal and nocturnal animals, passerine and non-passerine birds, fishes specialized and unspecialized for sound pressure reception, species arranged by size, etc.

FREQUENCY DISCRIMINATION

Fig. C3-0 presents the ranges of frequency discrimination thresholds for the lateral line system, fish, birds, and mammals. There is little evidence here for the notion of a phylogenetic trend in frequency discrimination capacity. Three of the most sensitive mammal species (elephant, human, and porpoise) are shown individually.

CRITICAL MASKING RATIO

Fig. C4-0 plots together all species for which critical masking ratio functions of frequency exist. There is little evidence for a phylogenetic trend in frequency selectivity as measured by the critical masking ratio.

INTENSITY DISCRIMINATION

Figs. C5-0 and C6-0 show intensity discrimination thresholds as functions of frequency and intensity for all species represented by a fairly complete data set. There is no phylogenetic trend. Generally, intensity discrimination is independent of frequency and declines with increasing intensity ("near miss" to Weber's Law).

TEMPORAL RESOLUTION

Fig. C7-0 shows noise and tone temporal modulation transfer functions for the several vertebrates that have been tested.

Fig. C8-0 shows gap detection thresholds for several species plotted as a function of the effective listening bandwidth.

Fig. C9-0 presents data on the discrimination of changes in sound pulse repetition rate for several vertebrates. There is no phylogenetic trend. The functions tend to obey Weber's Law.

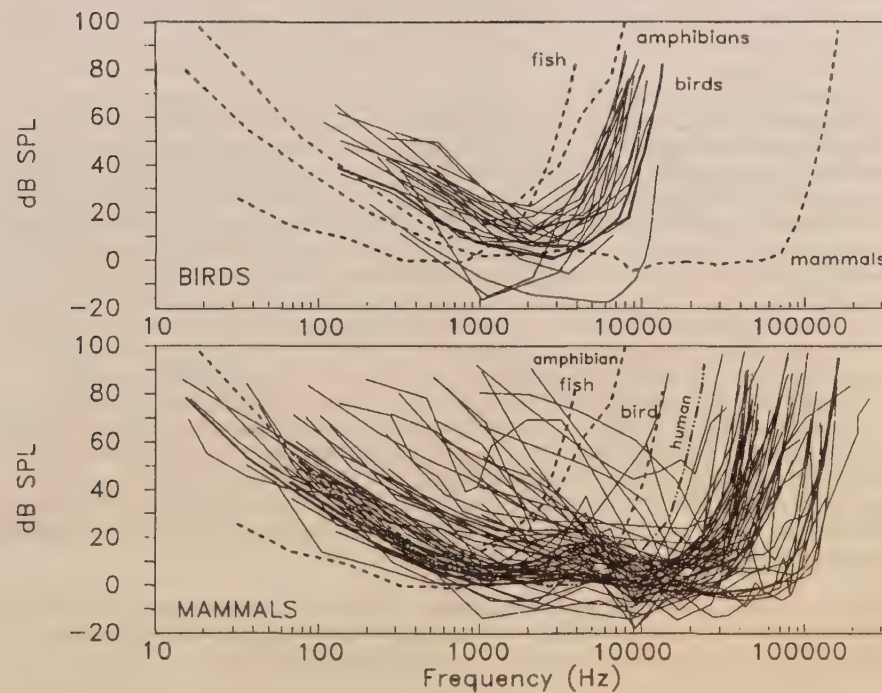
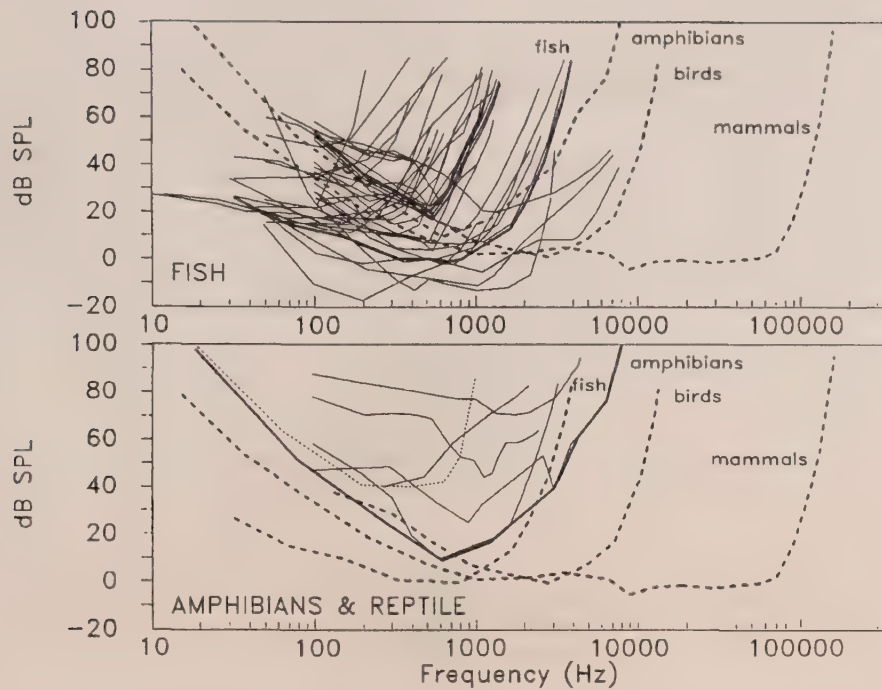
Fig. C10-0 presents data on duration or time interval discrimination. Some of the repetition rate discrimination data from Fig. C9-0 are recast as interval duration thresholds for this figure. There is no phylogenetic trend, and Weber's Law tends to hold.

PSYCHOPHYSICAL TUNING CURVES

Fig. C11-0 compares psychophysical tuning curves in simultaneous masking for a number of vertebrates. All vertebrates tested show qualitatively similar "auditory filters" by this measure.

Fig. C12-0 compares psychophysical tuning curves in simultaneous masking for chinchilla, from four different studies, with forward masked functions from one of the studies. Whether or not forward masking results in more narrow tuning curves for the chinchilla remains unclear.

Fig. C13-0 compares forward and simultaneously masked psychophysical tuning curves in human, monkey, chinchilla, parakeet, and two fish species. In general, forward masking produces more narrow functions in mammals and birds. Conclusions for fish are not yet clear.



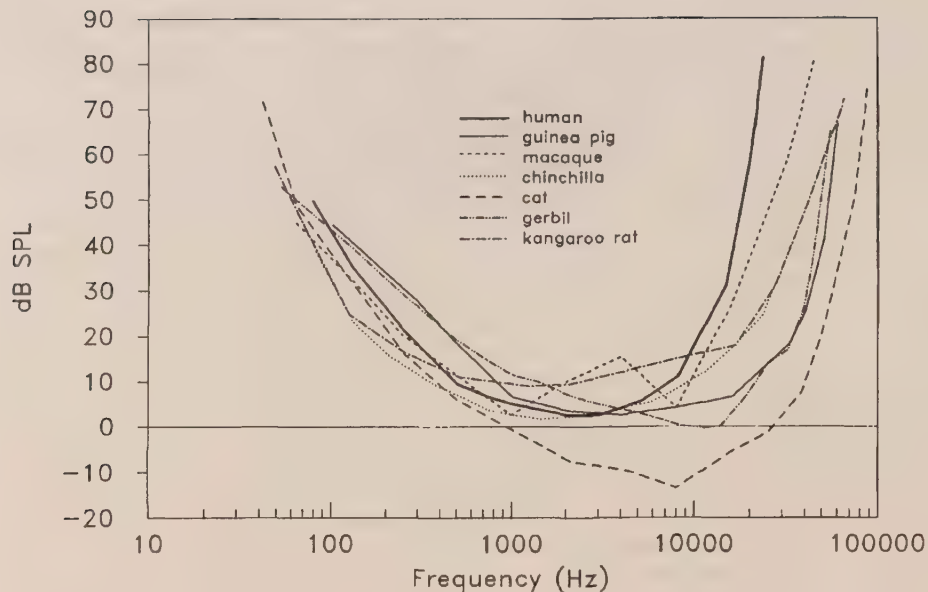


Fig. C1-0. (Facing page) Audiograms for all vertebrate species having valid audiograms. Heavy line encloses the threshold points, excluding about 10% of the lowest thresholds, providing a reasonable envelope for the hearing range of each group. The envelope lines appear in all panels. Where multiple audiograms exist for the same species, a median curve was defined graphically. Note similar sensitivity across all groups.

Fishes: (F1-0 to F11-0) Thresholds in dB relative to sound pressure levels in air corresponding to the sound intensity levels (in Watts m^{-2}) in water at threshold. There is diversity in best sensitivity and high frequency hearing. The group showing best high frequency sensitivity are the "hearing specialists" having some connection between the swimbladder and ear. Fishes without swimbladders not included.

Amphibians and Reptile: (A1-0 to A6-0) The one reptile (turtle) is shown dashed. The envelope is defined primarily by the bullfrog and green tree frog obtained using a sensitive method. The other higher thresholds are likely not valid estimates of hearing sensitivity. Amphibians hear within the same range as the fishes.

Birds: (B1-0 to B10-0) The birds are quite homogeneous in hearing sensitivity and bandwidth, with exceptionally low thresholds for the barn owl, crow, and great horned owl. The barn owl is unique among birds for its sensitivity at high frequencies.

Mammals: (M1-0 to M34-0) Mammals show the greatest diversity in best frequency and bandwidth, with elephant and human showing poorest high frequency sensitivity, and the echolocating mammals showing the best. Species differences in upper limit are about 1.5 decades (4.5 octaves). Low frequency hearing varies about 2.5 decades (9 octaves), due primarily to the poor low frequency hearing of echolocators and some of the rodents. Most mammals share a hearing range centered at 12 kHz. Many mammals show reduced sensitivity at 4-6 kHz.

Fig.C2-0. (Above) Audiograms for mammals often used in auditory research with good low frequency hearing. Human, M1-0; macaque, M3-0 (median); cat, M11-0 (median); chinchilla, M16-0 (median); kangaroo rat, M20-0; gerbil, M24-0.

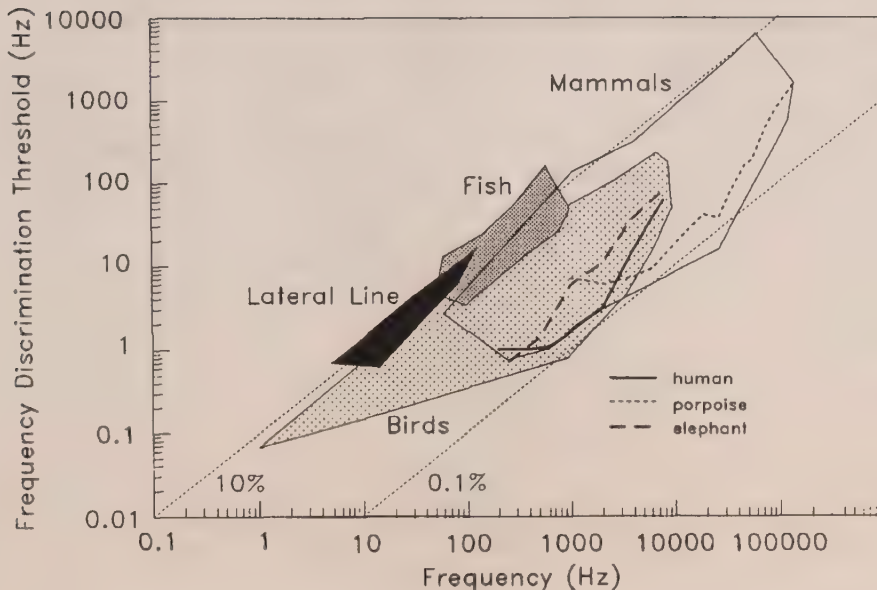


Fig. C3-0. A comparison of the frequency discrimination thresholds for all vertebrates that have been tested. Note the wide range of variation within a group at any given frequency (up to a factor of 100, or 0.1 to 10%).

Lateral line: (L3-0) These data from a fish and an amphibian range from about 4 to 15% between 5 and 100 Hz.

Fishes: (F38-0 and F39-0) Frequency discrimination for the fishes ranges from about 3 to 20%, appearing as an extension of the lateral line thresholds up to 1 kHz. Fishes clearly fall at the upper margins of the distributions for birds and mammals. It is likely that frequency discrimination for both the lateral line system and the fish ear is based on the processing of the sound waveform in the time domain without the possible benefit of well tuned peripheral channels.

Birds: (B37-0 to B39-0) In general, frequency discrimination in birds is comparable with discrimination in mammals, except for the limitation in hearing bandwidth characteristic of birds. The low frequency tail of this distribution encloses discrimination thresholds for the pigeon at "infrasonic" frequencies.

Mammals: (M63-0, M64-0, M65-0, M66-0, M68-0) Mammals overlap birds and fish in frequency discrimination abilities. The human curve helps define the lower limit of the mammal range and also corresponds to the thresholds of the most sensitive birds. Human frequency discrimination abilities are exceeded by the elephant at low frequencies, and by the porpoise at high frequencies. Within the range of vertebrate frequency discrimination capacities, the human is quite sensitive within its hearing range, but not uniquely so.

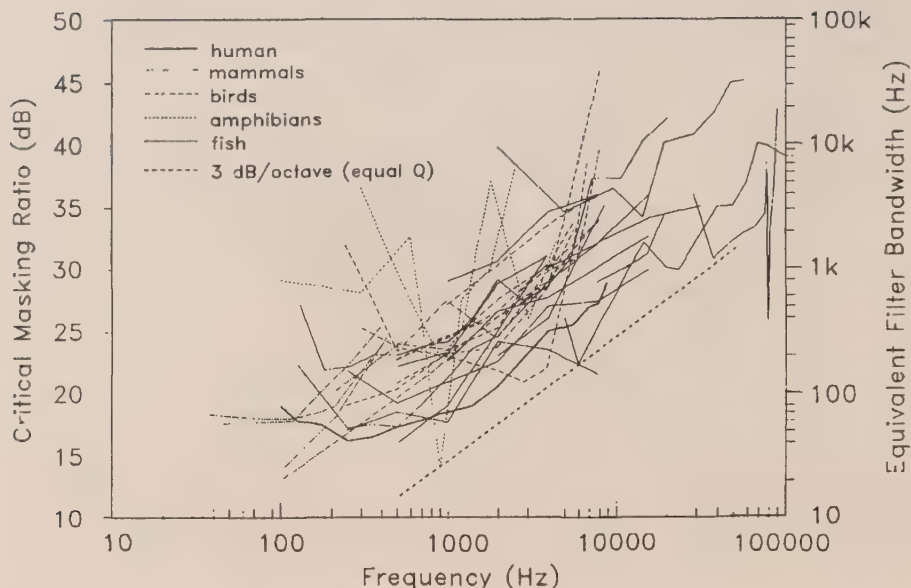


Fig. C4-0. Critical masking ratios (CR) for all vertebrate species tested. These thresholds derive from experiments in which pure tones are detected against a background of wide band noise. The threshold is defined as the sound pressure level of the tone at threshold minus the level of the noise in a one Hz band surrounding the signal frequency. The equivalent bandwidths were calculated as $10^{(CR/10)}$. The assumptions here are that only frequency components in the vicinity of the signal frequency are effective as maskers, and that the power of the noise within the effective band of the detection filter is equal to signal power at threshold. The latter assumption is likely wrong. The ratio of noise to signal power within the detection bandwidth can be estimated using the noise intensity discrimination threshold which varies among species. Some of the species variation in the CR may reflect differences in intensity processing as well as in detection filter bandwidth.

In general, CRs tend to increase with signal frequency, roughly at about 3 dB per octave. This slope would be expected if detection filters were "constant Q," or having a bandwidth proportional to center frequency.

Fishes: (F22-0 and F23-0) Several curves were smoothed. CRs for fishes fall well within the range of vertebrate variation, and tend toward the 3 dB per octave slope.

Amphibians: (A9-0) These two functions show both extremely large and extremely small CRs. The largest values (at high frequencies) are likely poor estimates since they suggest an effective masking bandwidth larger than the entire hearing range.

Birds: (B13-0 and B14-0) Bird CRs are rather alike, falling at the center of the mammal range. The exception is the parakeet data which declines up to about 3 kHz. This is a replicated finding, and these CRs correspond well to critical bandwidth estimates and with psychophysical tuning curve estimates of frequency selectivity.

Mammals: (M41-0 and M42-0) Mammals are quite diverse in CRs. Humans define the lower limit of CRs, and as in frequency discrimination, the porpoise data are an extension of the human data. The non-monotonic function at 80 kHz is for the greater horseshoe bat, well known for a specialized cochlear filter in this frequency range.

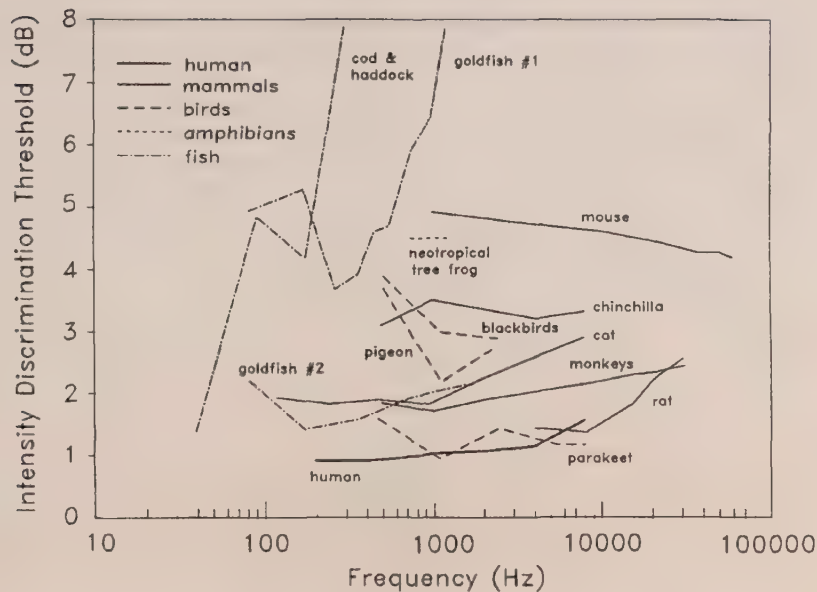


Fig. C5-0. Intensity discrimination thresholds as a function of pure tone frequency in vertebrates. The data plotted are for the species for which relatively complete data exist. Additional comparative data can be found in the text.

These thresholds plot the decibel difference in level between two pure tone bursts of the same frequency that can be reliably discriminated.

Human, cat, Old World monkeys, M39-0; rat, chinchilla, mouse, M40-0; parakeet, pigeon, blackbirds, B12-0; neotropical tree frog, A7-0; goldfish, haddock & cod, F19-0.

Among fishes, birds, and mammals, there is considerable variation in the intensity discrimination threshold among species and among studies. As a result, there is no evidence that fishes, birds, and mammals differ from each other, or can be ordered according to capacities for intensity discrimination.

In general, intensity discrimination seems to vary little with frequency. The lowest thresholds reported (between 1 and 2 dB) are for the human, parakeet, monkey, and goldfish.

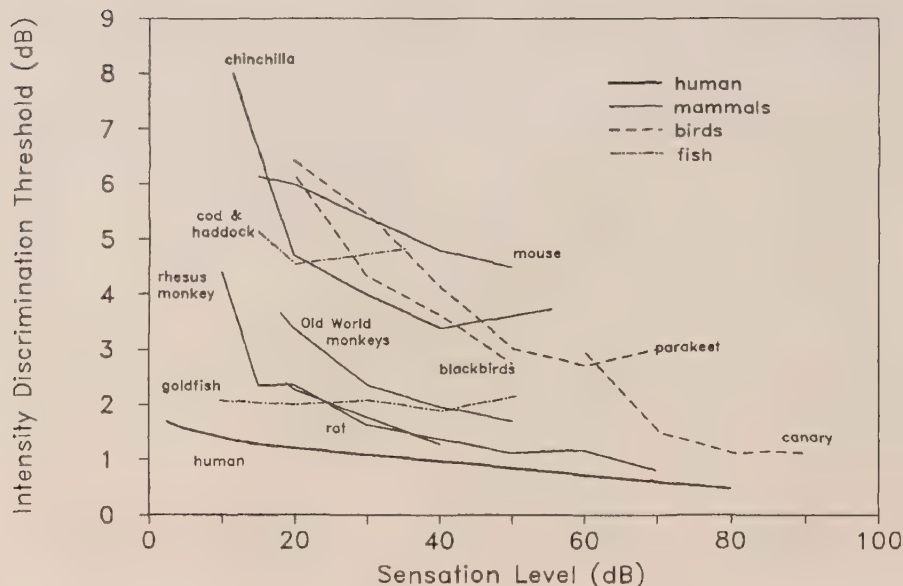


Fig. C6-0. Intensity discrimination thresholds for tones as a function of intensity in vertebrates. For some of these functions, data obtained for different tone frequencies have been averaged.

Human, Old World monkeys, rhesus monkey, M36-0; chinchilla, mouse, rat, M37-0; parakeet, canary, blackbirds and pigeon, B11-0; goldfish, F20-0.

Large differences are seen among species and studies, but there is no evidence that birds, fishes, and mammals differ from one another in any clear way. The lowest thresholds shown are for the human, monkey, parakeet, and goldfish.

In most all species, there is a tendency for the intensity discrimination threshold to decline with increasing sensation level. This has been termed a "near miss" to Weber's Law. Weber's Law states that the just detectable increment in stimulus intensity (ΔI) is a constant proportion of the base intensity, or $\Delta I/I=k$, where k is a constant. This predicts that the intensity discrimination threshold should be constant in dB, since a given decibel difference is proportional to the ratio of the two stimulus levels which are just discriminably different. It is important to note, however, that the "miss" to Weber's Law is small, and that the "near hit" is a fundamentally more important fact than the "near miss."

The species showing the best approximation to Weber's prediction is the goldfish. Note, however, that the goldfish also "misses" considerably in detecting amplitude modulation impressed on continuous pure tones (Figs. F45-0).

In general, Weber's Law holds to a greater extent for noise intensity discrimination than for tone intensity discrimination.

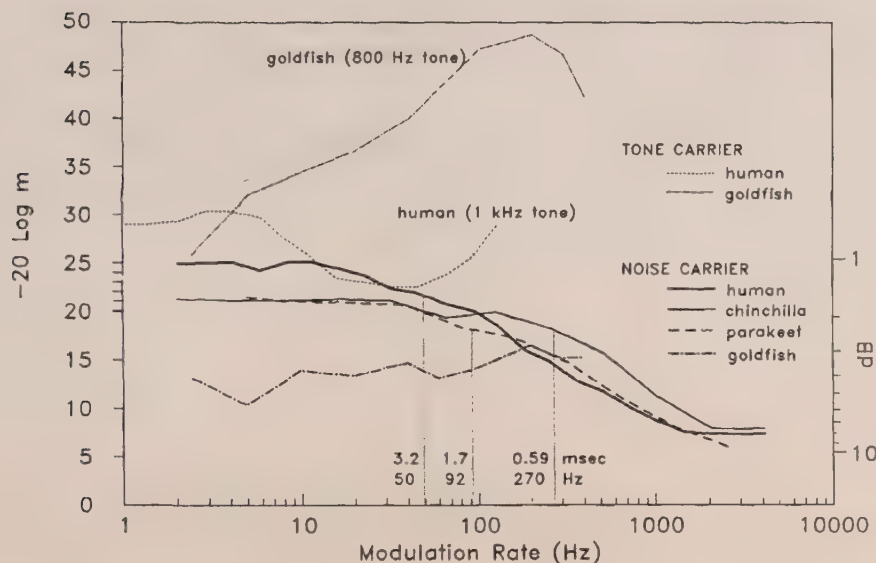


Fig. C7-0. Thresholds for the detection of sinusoidal amplitude modulation impressed on pure tones and broad band noise as a function of modulation frequency.

Human, M84-0; chinchilla, M84-0 (Mean of two functions); parakeet, B43-0; goldfish, F43-0.

The four noise functions have been termed temporal modulation transfer functions (TMTF). Modulation detection thresholds are plotted as $-20\log(m)$, where m is the modulation index required for the observer to discriminate a modulated from an unmodulated signal. Modulation index (m) is defined as $(P-T)/(P+T)$, where P is the sound pressure at an envelope peak, and T is the sound pressure at a trough in the envelope. The right hand ordinate indicates the corresponding intensity difference (in dB) between P and T .

Noise TMTFs have been used to define the characteristics of an hypothetical filter which limits the internal representation of the modulated envelope. For the human, chinchilla, and parakeet, the 3 dB-down points (F , in Hz) on the functions are indicated along with the equivalent time constants (in msec). The time constant is defined as $(2\pi F)^{-1}$. These cut-off frequencies and time constants vary considerably among the three species. The lower cut-off frequency for the human is associated with high sensitivity to modulation at the low modulation frequencies where modulation detection can be equated with a noise intensity discrimination task. The goldfish is considerably less sensitive in detecting amplitude modulation in noise compared with the other species, and gives a fundamentally different modulation detection function.

Detection of modulation on tones is shown for the human and the goldfish. These are fundamentally different functions. At the lowest rates, thresholds can be viewed as intensity difference thresholds. As modulation frequency rises, the spectral side bands may be independently detected, providing a spectral cue for modulation detection. This likely accounts for the rise in sensitivity of the human curve at about 50 Hz. The goldfish function is not easily explained, showing a continuous growth in sensitivity with modulation frequency, exceeding human sensitivity above 10 Hz.

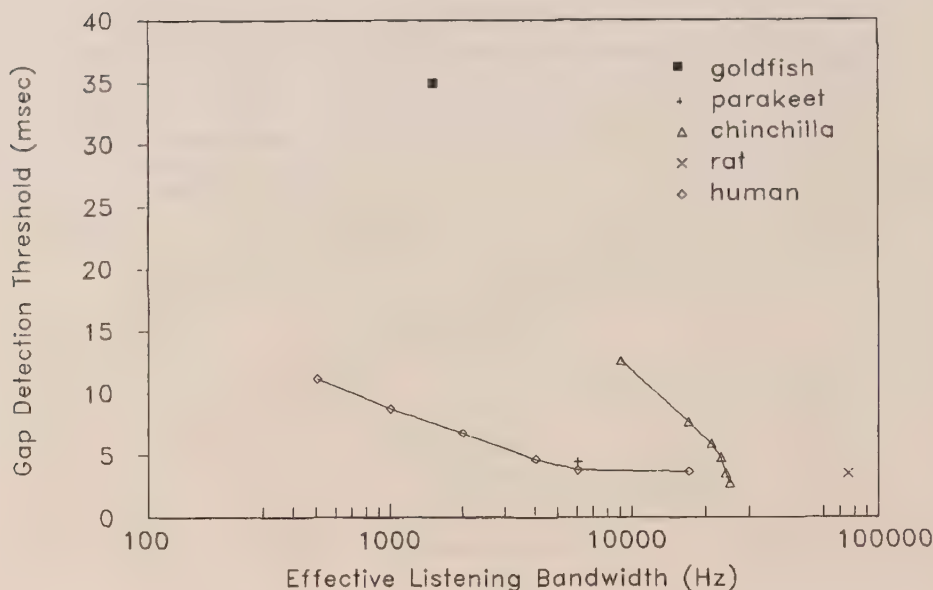


Fig. C8-0. Gap detection thresholds as a function of effective listening bandwidth in several vertebrates. These thresholds define the shortest temporal gap or silent period occurring in wide band noise (40-50 dB sensation level) that can be detected. This is a measure of the temporal resolution of the auditory system for processing envelope decrements.

Human, (Fitzgibbons, 1983. See also M85-0); chinchilla, M86-0; rat, M85-0; parakeet, B43-0; goldfish, F21-0.

For the human data, effective listening bandwidth was defined by low-pass filtering the noise with cut-off frequencies indicated on the abscissa. For the chinchilla, bandwidth was restricted by pre-exposing the animals to high-pass filtered noise (causing a frequency-specific temporary threshold shift) with cut-off frequencies indicated on the abscissa. For the human, chinchilla, rat, and parakeet, the minimum detectable gaps fall in the 3-4 msec range. For the human, this corresponds to the time constant derived from the noise TMTF (Fig. C7-0). The 35 msec minimum detectable gap for the goldfish may be partly due to the narrow hearing bandwidth of this species.

The gap threshold also rises at lower sensation levels (M85-0), and is larger for observers with sensorineural hearing loss. Gap thresholds as large as 35 msec can be observed in some human observers with sensorineural hearing loss.

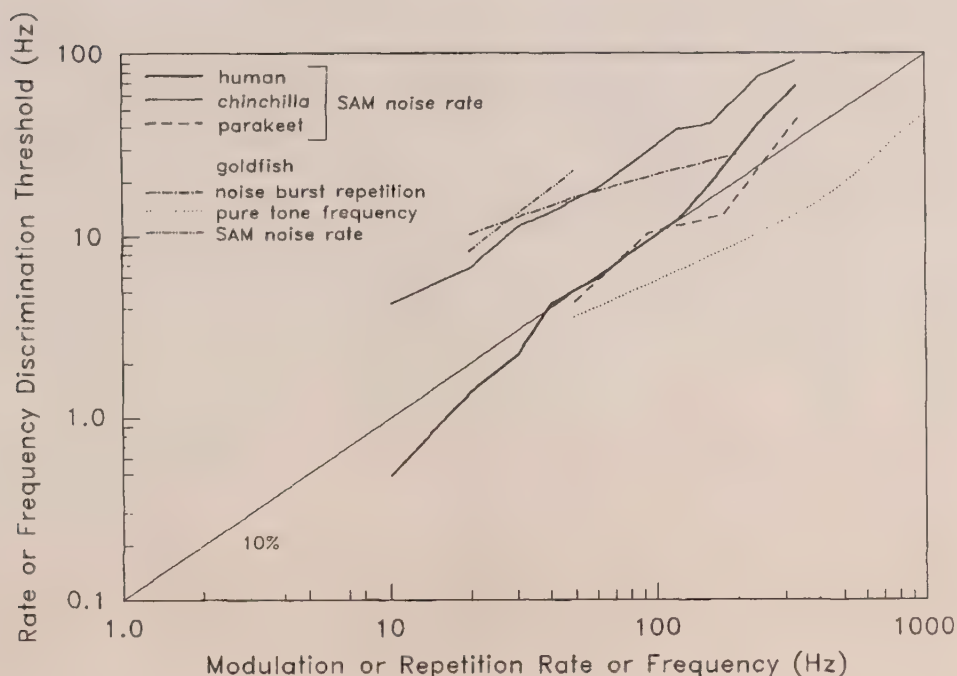


Fig. C9-0. Thresholds for the discrimination of changes in the repetition rate or frequency of periodic envelopes or waveforms. These are measures of the accuracy with which temporal intervals are represented in the auditory system.

Human and chinchilla, M81-0; parakeet, B42-0; goldfish, F47-0.

The human, chinchilla, parakeet, and one of the goldfish functions were obtained using 100% sinusoidally amplitude modulated (SAM) noise. The human and parakeet show quite similar thresholds (about 10%). The goldfish and chinchilla show similar but considerably higher thresholds compared with the human and parakeet.

Goldfish were also tested using repeated, brief noise bursts. These thresholds decline, relatively, toward the higher repetition frequencies. For comparison, goldfish pure tone frequency discrimination thresholds are plotted. It is thought that pure tone frequency discrimination in the goldfish is based on the processing of temporal neural intervals.

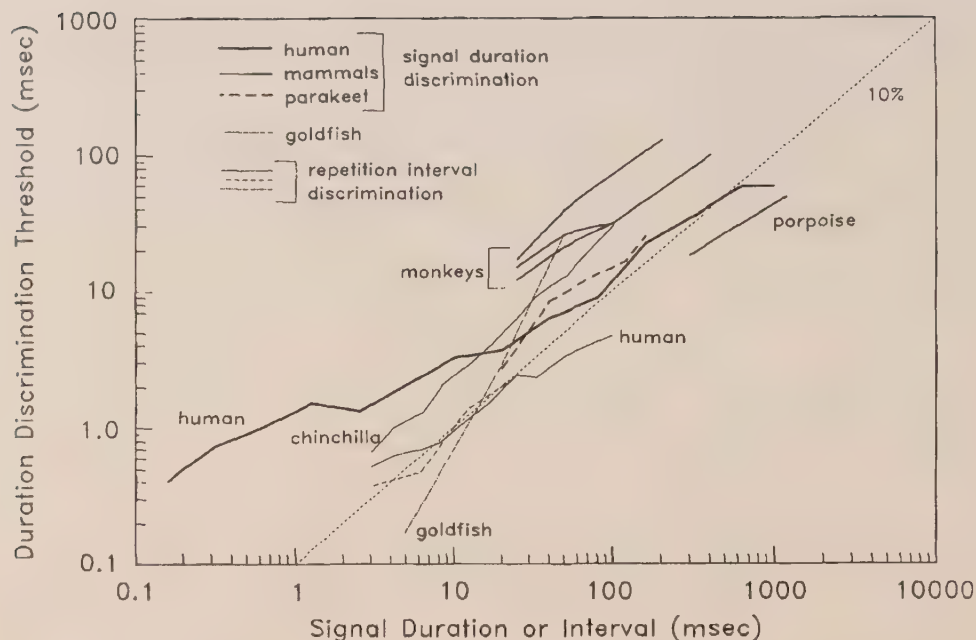


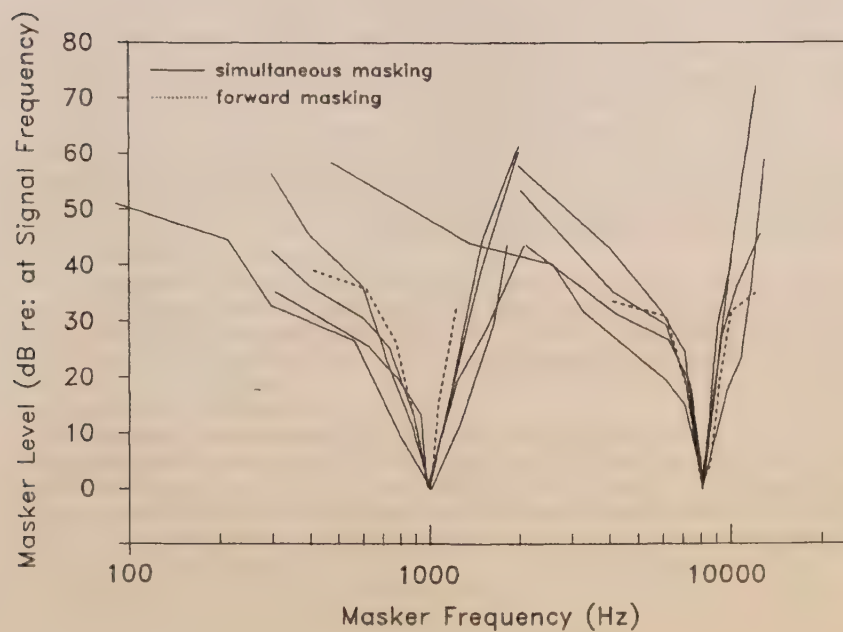
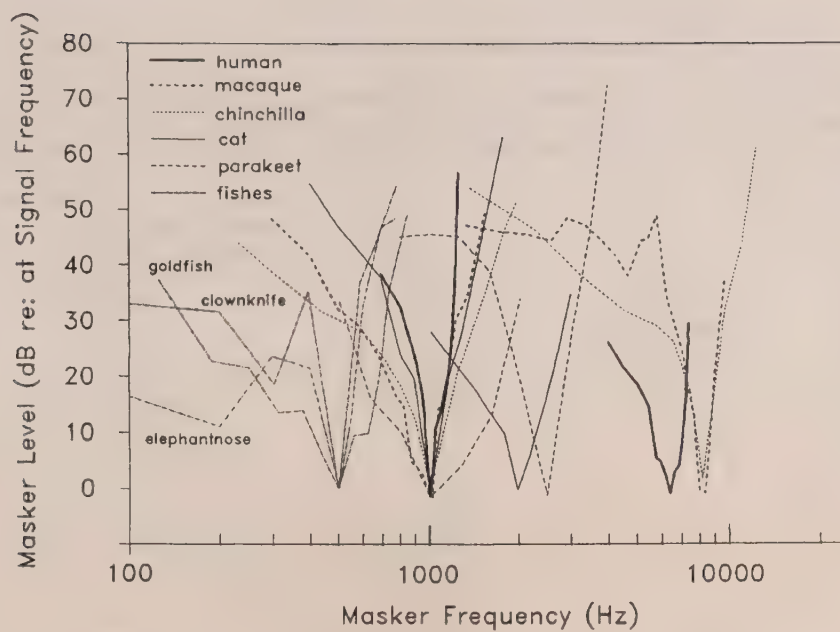
Fig. C10-0. Duration discrimination thresholds for several vertebrate species compared with repetition interval discrimination thresholds.

Duration discrimination: Human, monkeys, porpoise, and chinchilla, M82-0; parakeet, B42-0.

Repetition interval discrimination: Human and chinchilla, M81-0; parakeet, B42-0; goldfish, F47-0.

In general, duration discrimination thresholds tend to obey Weber's Law in that the just discriminable difference in duration tends to be a constant proportion of the base signal duration (7 to 20%). The data for humans deviate from this relation at the short durations. Human and parakeet duration discrimination are quite similar. The porpoise shows the lowest thresholds at the long durations.

Thresholds derived from repetition interval discrimination studies tend to be lower at short intervals (at high repetition rates), and the goldfish is unique in showing a function with approximately twice the slope of the other species tested.



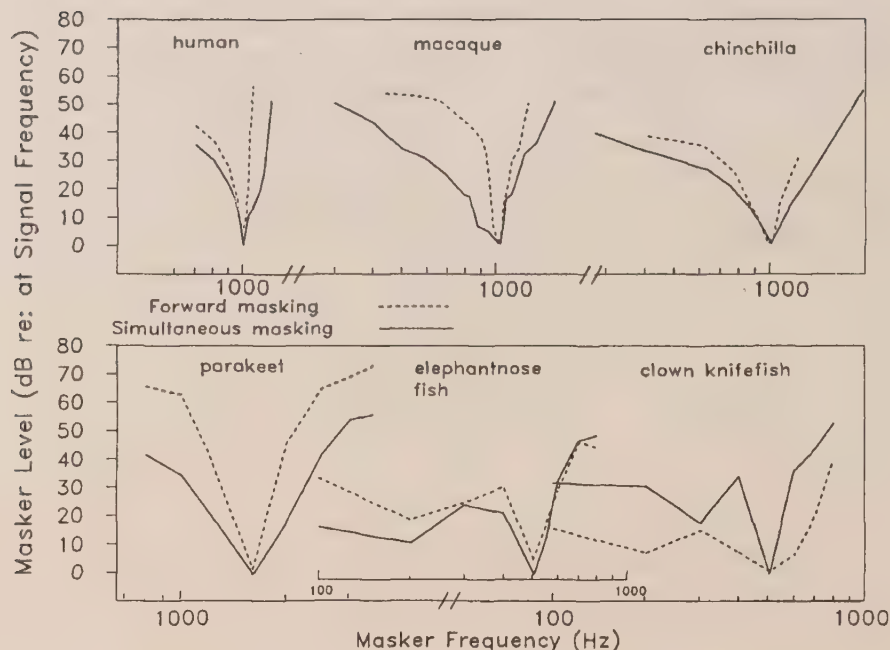


Fig. C11-0. (Facing page, top) Psychophysical tuning curves in simultaneous masking for several vertebrates. All vertebrates tested show band-pass filter functions centered on the signal frequency.

Goldfish, F32-0 (PTC at 400 Hz signal transformed by equal frequency ratios and plotted at 500 Hz); clown knifefish, F34-0; elephantnose fish, F30-0; macaque, M57-0; human, M60-0; cat, M56-0 (median); chinchilla, M50-0, M51-0, M52-0, M53-0 (median); parakeet, B23-0.

At 1 kHz, the human shows the most selective tuning, and the parakeet the least. In the 2 kHz region, the cat and parakeet show comparable selectivity. In the 6 to 8 kHz region, the macaque and chinchilla show greater selectivity than the human. The three fish species studied show similar high frequency roll-offs, but differ in complex ways below signal frequency.

Fig. C12-0. (Facing page, bottom) Psychophysical tuning curves in simultaneous masking and forward masking (dashed) in the chinchilla. Simultaneous curves from M50-0, M51-0, M52-0, and M53-0. Forward masking curves from Fig. M51-0. In general, forward masking functions seem slightly more sharply tuned than in simultaneous masking.

Fig. C13-0. (Above) Psychophysical tuning curves in forward and simultaneous masking for the human (M60-0), macaque (M57-0; M58-0), chinchilla (Simultaneous; median from C12-0. Forward; M51-0), parakeet (B31-0), elephantnose fish (F30-0), and clown knifefish (F34-0). In all birds and mammals, forward masking tuning curves are more sharply tuned. Generalizations for fish cannot be made.

COMBINED TOPICAL INDEX

For major topics, animal groups are listed separately under their own headings. In all cases, record numbers beginning with L, F, A, B, and M refer to data for Lateral line, Fish, Amphibians and reptiles, Birds, and Mammals, respectively.

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